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FIBRE ANALYSIS OF THE ANTERIOR AND LATERAL FUNICULI OF THE CORD IN THE CAT

G. T. VAN BEUSEKOM

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AAN MIJN VROUW
AAN MIJN OUDERS

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CHAPTER I.

INTRODUCTION.

The white matter of the cord is composed of large numbers of fibres, both ascending and descending, which have their origins in nearly all levels of the central and peripheral nervous system. These fibres present for the greater part the same morphological aspect, however, one sees differences in size and myelinisation. Myelinated fibres possess either a distinct myelin-sheath or there are other fibres in which this sheath is either very thin or non-existent. These latter fibres are generally considered to be unmyelinated fibres. Fibres of different sizes have different conduction velocities. Sensory fibres of a certain diameter usually mediate a special modality of sensation. However, no morphologic differences between sensory and motor fibres are known, neither is anything known about the function of motor fibres of different sizes.

In 1936 H ä g g q v i s t initiated fibre analysis as a means of examining the content of the white matter of the cord and other parts of the nervous system. Before that time attempts at fibre analysis had been done almost exclusively with methods *which could not show the size and shape of each separate fibre of the white matter*. These attempts therefore were rather unsuccessful. H ä g g q v i s t's technique was an entirely new approach and it opened almost unlimited possibilities. Until recently it was only occasionally used. It seems worth while to use H ä g g q v i s t's method in a study of the spinal cord, in order to determine with precision where the fibres of the different tracts, at different levels, are located.

In this study, the cord of the cat was chosen for various reasons. The cat is easily available, it is neither too small nor

too large and also the organization of its central nervous system is not too primitive (even though the cat is not a primate). Furthermore, the cat is largely used as a laboratory experimental animal and as far as I could find, no atlas of the white matter of the cord of the cat exists. Recent studies (Verhaart 1953) have revealed that the structure of the spinal white matter of the cat is relatively easy to study, since a number of tracts stand out conspicuously because of their high contingent of thick fibres. In view of the above-mentioned facts it is my opinion that the application of Häggqvist's technique to the cat's cord might give additional information on the anatomy of the cord.

Häggqvist in 1936 and after him a small number of other authors, have demonstrated that *most fibresystems and fibretracts are characterized by their fibrepattern* (each tract is composed of definite proportions of fibres of various diameters). This pattern is preserved within certain limits throughout the course of the tracts in the central nervous system. The tracts can be identified and followed once one has an appreciation of their fibrepatterns.

In the laboratory of Histology and Microscopical Anatomy at Leyden, Häggqvist's technique has been introduced as the routine technique for the study of the pathways and fibretracts of the central nervous system. Its chief advantage over more classical methods is that *it shows both the axon and the myelinsheath of each separate fibre.* Even fibres of less than one μ in diameter can be demonstrated. Moreover, the stain *shows degenerating fibres very distinctly,* as such, and therefore in cases of severance of a pathway both the affected and the preserved fibres can be studied in the same preparation.

Only the lateral and the anterior funiculi of the cord will be the subject of this thesis. Because they are almost completely isolated from the posterior funiculi, they can be dealt with separately and because they fuse and interchange fibres extensively they have to be considered as a whole.

For practical purposes the white matter of the cord is divided into:

the anterior funiculus, which extends from the ventral longitudinal fissure to the most lateral rootlet of the anterior root;
the anterolateral funiculus, from the lateral border of the anterior funiculus to a horizontal line from the intermediate horn laterally; and
the posterolateral funiculus, from that line to the posterior horn and the posterior root. The word funiculus will be used exclusively in connection with the white matter, the word horn in connection with the grey matter.

As is already generally known, the position of the different tracts, as well as the sizes of the areas they occupy, may change during their course through the cord and therefore, the structure of the cord at the various levels may differ considerably. It is obvious that the cord can not be studied without taking these changes into consideration and therefore, the white matter throughout the whole extent of the cord will be examined. The caudal part of the medulla has to be included because its structure resembles that of the upper cervical cord and many tracts can much more easily be identified in the medulla than in the cord. This is because of the fact that in the cord the tracts all run in the same direction and form one body of white matter, whereas in the medulla some deviate from their longitudinal course and others are separated by grey matter and fibrebundles running transversely. Besides this, following tracts through the transition of the medulla into the cord can give information concerning the topographical relations of the pathways in the cord, not obtainable when examining the cord alone.

CHAPTER II.

SURVEY OF THE LITERATURE.

There is a considerable amount of literature on the fibre-tracts in the cord. Many of the papers do not deal with the cord as such, but only with one or other of its fibretracts. The course of these tracts is only described through the brain stem and the cord. It is almost impossible, therefore, to give an account of all the papers in which the position of a tract in the cord is indicated. On the other hand atlases of the cord of animals seem to be extremely rare. The well-known atlases confine themselves to the brain stem and do not go beyond the level of the pyramidal crossing or the first cervical segment. There are many pictures of the segments of the cord of man in the textbooks, but they do not seem to be reliable since they differ considerably in the location of a number of tracts. Besides this, they give so few details that they are of little value to neurosurgeons and experimental workers. The old literature will not be reviewed as it is not of direct interest in regard to the scope of this thesis.

Since papers in the most part do not emphasize possible differences in structure between the cord of the animal under consideration and of man, papers about the cord of both lower animals and man will have to be taken into account. From the lower animals the M a c a c a monkey is frequently used in neuro-anatomical and neuro-physiological experiments. Papers dealing with this monkey's cord, therefore, will be especially reported.

THE HUMAN CORD.

The human cord has been studied most of all; a number of pictures of its segments can be found in almost all text-

books. As already stated, most of them are only moderately reliable because large differences between the site attributed to the tracts are to be found among them and because they are largely based on animal experiments. Most of the papers about the anatomy of the human cord are based on human pathological material. Only a survey of the different tracts, as they are described by the various investigators, will be offered.

In 1928 Bok gave the following account of the fibre structure of what he called the anterolateral funiculus. His leading principal was Flatau's law, which states that *long ascending, as well as descending fibres, have their course at the periphery of the cord, whereas the shorter ones have a more central course.* He pointed out that *every fibre* originating in the spinal grey matter *has a spiral course from its origin to its definite site in the tract* to which it belongs. Short fibres run a narrow spiral close to the grey matter, large ones make a wide spiral close to the outer surface of the cord. He assumed a sharp boundary to be present between the ascending dorsal spinocerebellar tract and the descending lateral corticospinal tract. This he attributed to the difference in phylogenetic age and functional character of both tracts. On the contrary, no such sharp demarcation exists between the tracts of the anterolateral funiculus because of their common origin in the cord. Flechsig's tract extends ventrally into Gowers' area, which contains the major part of the ventral spinocerebellar tract. He states that where Flechsig's and Gowers' tracts touch in the upper part of the cervical cord, the lateral pyramidal tract does not reach the surface of the cord. In these tracts also the longer fibres are situated more peripherally than the shorter ones. The lateral pyramidal tract nowhere extends ventral to a line running from the intermediate horn laterally. During its course it is considered to receive fibres from the anterior pyramidal tract, which disappears in the upper part of the thoracic cord. The shortest intraspinal fibres have their course in the cornumarginal area which surrounds the grey matter. The spinal sympathetic fibresystem is composed

of the nucleus intermedio-medialis and -lateralis, connected by means of the mediolateral tract. The intermedio-longitudinal tract originates from and connects the different levels of the nucleus intermedio-lateralis.

In 1951 Bok stated that the posterolateral funiculus, from medial laterally, contains in the following order: the intermedio-longitudinal tract, the reticulospinal tract, the dorsal vestibulospinal tract, the rubrospinal tract, the tectospinal tract and finally the lateral pyramidal tract. These tracts are considered to fill the whole triangle formed by the posterior horn, the dorsal spinocerebellar tract and the horizontal through the intermediate horn. Bok emphasized the fact that the fibredistribution differs considerably at different levels of the cord, but he did not give details and described mainly a high cervical level.

In 1939 another account of the fibresystems in the spinal cord was given by Max Clara. He also described a cornumarginal area and firmly committed himself to the law that long fibres run peripherally. He concluded, therefore, that a sharp localization was present in the lateral corticospinal tract and even indicated lamellas of fibres going to the motor neurons which innervate a certain musclegroup. In the anterolateral area he described the lamellation indicated, and from medial to lateral he gave the localization of sensibility modalities in the order of: pressure, touch, pain and temperature. He considered the reticulospinal tract to be present as scattered fibres only, and the rubrospinal tract to be of no significance in man.

When comparing two recent textbooks of neuro-anatomy (Ranson and Clark—Mettler) I found that they appear to agree about many points and to differ about others. They attribute the same localization to the dorsal and ventral spinocerebellar tracts. However, Ranson and Clark indicate that the ventral spinocerebellar tract arises from cells at the base of the dorsal horn and from the intermediate horn. Mettler, in accordance with Cooper and Sherrington, writes that the tract arises from the bordercells of the lumbar ventral

horn. He also states that the ventral spinocerebellar tract arises more caudally in the cord than Flechsig's tract and that they convey impulses from the lower and from the upper extremity respectively. Ranson and Clark are of the opinion that the dorsal spinocerebellar tract appears in the first lumbar segment, whereas the ventral spinocerebellar tract is already visible in more caudal segments. They point out that both spinotectal and spinothalamic fibres ascend in Gowers' tract.

Ranson and Clark indicate separate areas for the tracts, except the vestibulospinal and ventral spinothalamic tract, which overlap comlpetely. They stress the fact however, that no tract has a sharp border, but that adjacent tracts intermingle at their borders. They admit that the exact location of many tracts is not quite established.

Mettler, on the contrary, in a diagram, shows considerable overlapping of most tracts. The tracts occupy for the greater part a larger area than in the diagram of Ranson and Clark. In his diagram the spinothalamic fibres occupy all of the anterolateral funiculus, the ventral spinocerebellar tract excepted, and the lateral part of the anterior funiculus. He agrees with Walker that the lateral spinothalamic tract mainly conveys thermal impulses, the ventral tract tactile ones and the fibres, in between, painful ones.

In their text Ranson and Clark are of the same opinion, but in their diagram the ventral and lateral spinothalamic tracts are wide apart. Both textbooks mention the segmental localization in this system and localize the sacral segments dorsolaterally, the cervical segments ventromedially, and the other segments in the same order in between.

Mettler denies the existence of spino-olivary fibres, but Ranson and Clark accept the existence of spino-olivary as well as olivospinal fibres, which are localized in Helweg's triangle. Both Ranson and Clark and Mettler indicate a spinotectal tract in the area of the lateral spinothalamic tract.

No difference of opinion exists with regard to the lateral crossed, as well as the ventral uncrossed, corticospinal tract.

The rubrospinal tract is of no great importance in man, according to Ranson and Clark. They localize rubrospinal fibres ventral to the lateral pyramidal tract. Mettler, on the contrary, attributes a large area to this tract. The fibres descend to the sacral segments and in the lower cervical segments they occur in the whole posterolateral funiculus, scattered among other fibres of this area.

Ranson and Clark indicate the vestibulospinal tract of Deiters only in the anterior funiculus, but Mettler mentions uncrossed vestibulospinal fibres, situated in Deiters' tract, and crossed ones which descend in the medial longitudinal fascicle in the medulla as well as in the cord. These fibres descend to lumbar segments.

Among the medial vestibulospinal fibres, Mettler localizes a medial reticulospinal tract, and in the area of the rubrospinal and the lateral corticospinal tract a lateral reticulospinal tract (Papez). Ranson and Clark refer to Papez, but do not indicate reticulospinal tracts. They localize a tectospinal tract in the ventral part of the anterior funiculus. Mettler localizes the interstitiospinal tract of Cajal along the anterior medial fissure and a solitariospinal tract, originating in the tractus solitarius nucleus, which descends into the thoracic cord along the lateral border of the ventral horn.

None of these textbooks gives a detailed topography of the fibresystems in the different segments of the cord. They both show a broad area around the grey matter containing long and short intraspinal connections.

Riley, in 1943, published an atlas of the human central nervous system, in which many segments of the cord were pictured. Unfortunately he only used Weigert-Pal-stained slides, which do not show separate fibretracts clearly, especially in the spinal cord. The following survey of his statements can be given.

The first cervical segment: in the white matter, bordering the anterior medial fissure, just lateral to the ventral corticospinal tract, the following tracts, which in the medulla form

the medial longitudinal fascicle, are located; from dorsal ventrally there are the mesencephalo-spinal tract, identical to the interstitiospinal tract of Cajal, the medial reticulospinal tract and the tectospinal tract. In the anterior funiculus from medial laterally, under the pia mater, there are the medial and lateral vestibulospinal tract, and more laterally the triangular area of Helweg, containing the ventrolateral corticospinal tract, sympathetic fibres and possibly the olivospinal and spino-olivary fibres. Lateral to this triangle, along the surface of the cord, the spinotectal and the spinothalamic tract are situated. The dorsal and ventral spinocerebellar tracts are located in the dorsolateral funiculus, underneath the pia mater. The ventral spinocerebellar tract does not extend ventral to the intermediate spinal sulcus. The lateral corticospinal tract lies for the greater part within the reticular substance of the spinal grey matter, together with the lateral reticulospinal tract.

At the 2nd cervical segment topography is the same, with the exception of the lateral corticospinal tract, which has shifted to the centre of the posterolateral funiculus.

C_3 shows no great changes, neither does C_4. In C_5 there seems to be more space between the various tracts, especially the medial and lateral spinothalamic tract are wide apart.

At C_7 the medial spinothalamic tract is no longer indicated. The lateral one, together with the spinotectal tract, has moved somewhat dorsally and remains in connection with the ventral spinocerebellar tract.

At the first thoracic segment the ventral reticulospinal tract, in the anterior funiculus, can no longer be found. The spinocerebellar tracts have moved somewhat ventrally. From the lateral part of the anterior funiculus the Helweg area, with the ventrolateral corticospinal tract and spino-olivary fibres, is missing.

Th_2 does not differ from Th_1. The interstitiospinal tract is no longer indicated in Th_5, and gradually the other tracts decrease in size. Th_8 shows only the dorsal spinocerebellar tract, the ventral one having disappeared. At the ventral tip of the anterior funiculus the tectospinal tract is no longer found.

At Th_{12} all remaining tracts are much smaller and the dorsal spinocerebellar tract has shifted ventrally.

At the first lumbar segment the medial and the lateral vestibulospinal tract, together with the ventral corticospinal tract, have disappeared from the anterior funiculus. No tracts are indicated in this part of the white matter. L_2 shows clearly the small size of the remaining tracts viz.: the lateral corticospinal tract, the rubrospinal tract, the dorsal spinocerebellar tract, the lateral spinothalamic tract and the lateral reticulospinal tract. The tectospinal tract is found in the area of the lateral spinothalamic tract. In the next segment the lateral reticulospinal tract also has disappeared, and the dorsal spinocerebellar tract is not indicated either. The rubrospinal tract reaches its end at the fifth lumbar segment and the spinothalamic and spinotectal tracts disappear at the third sacral segment. The lateral corticospinal tract is the longest one in the human cord. It is still indicated in the fifth sacral segment.

In 1936 Häggqvist's first paper about the fibre structure of the central nervous system was published. In this study he used his modification of the Alzheimer-Mann methylblue-eosin technique. He gave the results of the counting and measuring of groups of fibres of the human cord in a cross-section at the third thoracic segment. He divided this cross-section in several areas of different fibrepatterns. Fibres were counted in groups of one μ difference in diameter. The smallest fibres, one μ thick, were far the most numerous. Fibres 6 to 8 μ in diameter were not very numerous and very thick fibres occured chiefly in both spinocerebellar tracts, as well as at the anterior border of the anterior funiculus. Many of Häggqvist's areas can be identified with well-known tracts. Area 1 is the anterior corticospinal tract, area 2 the medial longitudinal fascicle, area 4 comprises the anterior vestibulospinal tract and area 10 the lateral corticospinal tract. According to Häggqvist, area 7 contains spinothalamic fibres, whereas area 8 represents the ventral and area 11 the dorsal spinocerebellar tract. Unfortunately Häggqvist discontin-

ued this subject shortly afterwards and his method was employed only occasionally by others (Sjöqvist, 1938).

Szentagothai-Schimert (1941) also counted and measured fibres in a number of tracts using Spielmeyer's technique. The fibrespectrum of the lateral pyramidal tract at C_2 was: 1 μ in diameter 35 %, 3 μ 28 %, 5 μ 12 %, 7 μ about 13 % and over 7 μ less than 10 %. At Th_5, however, quite different figures were found: 1 μ 11 %, 3 μ 32 %, 5 μ 18 %, 7 μ 17 % and over 7 μ again less than 10 %. From his counts and measurements he concluded that long fibres, as well as early myelinating ones, are thick. According to him the fibrespectrum of a pure tract, graphically plotted, represents a normal distribution curve.

As for papers dealing with single fibresystems only the most important ones will be reported. They will be reviewed in groups dealing with the same tract, in chronological order.

The pyramidal tract.

When reviewing the literature dealing with the pyramidal tract we are struck by the huge number of papers. After Türck discovered the pyramidal tract in 1851, it was generally believed that it arose diffusely from the whole cerebral cortex. In the beginning of this century experiments by Grünbaum and Sherrington (1901) and Holmes and May (1909) clearly demonstrated that especially the large pyramidal cells of Betz in the gigantocellular area of the precentral cortex were the origin of the pyramidal tract. This became the common opinion until 1915 when a publication of von Monakow cast doubt on this opinion. He found that more than the motor area of the cerebral cortex had to be destroyed to give a complete degeneration of the pyramidal tract. Many new investigations were performed and it was recognized that Betz' cells could only with difficulty be differentiated from other cells in the motor cortex. Moreover, it was found that the pyramidal tract contains 30—40 times as many fibres as the highest estimated number of Betz' cells in the motor cortex (Lassek).

Lassek made a special study of the pyramidal tract, based upon observations in cats, monkeys and men. He came to the conclusion that *the pyramidal tract arises from a far greater area of the cerebral cortex than the part containing* Betz' *cells.*

Pyramidal fibres arise from the frontal, parietal and even the occipital lobe. Most pyramidal fibres, however, arise from the motor cortex, which consists of the areas 4, 4s and 6. Possibly the cells of Betz are the cells of origin only of the thickest pyramidal fibres. In the adult, the pyramidal tract in the medulla contains an average number of 688.800 myelinated fibres. Ninety percent of these fibres are between 1—4 μ in diameter and fifty percent of these do not surpass 1 μ, 1.7 percent of the total number of fibres are thicker than 10 μ (Lassek 1942, '47). Eleven months after a cerebral softening the medullary pyramid can be almost totally devoid of fibres, whereas in the cord normal fibres are present in ever increasing numbers, when descending in the cord. In the fifth thoracic segment these fibres number 20—30 percent in the lateral corticospinal tract and 5—10 percent in the ventral one (Lassek and Evans, 1946). This phenomenon has also been described in monkeys and cats. The authors suggest that the fibres are probably ipsilateral corticospinal ones. This, however, explains only partially their presence. The remaining fibres must be foreign fibres, either subcorticospinal and/or propriospinal.

Verhaart (1953) pointed out that it is hardly possible to speak of a pyramidal tract in the spinal cord, because its boundaries are indefinite and it contains many fibres of other origins.

The rubrospinal tract.

Von Monakow demonstrated the existence of the rubrospinal tract for the first time (1883), without knowing however, its origin and termination. Other investigators soon afterwards found that retrograde degeneration occurred in the magnocellular part of the red nucleus when its fibres were

severed. Because of these publications, based on animal experimentation, the rubrospinal tract has been assumed to exist in all mammals, but not much evidence supported its existence in man.

André-Thomas, in 1936, stated that he could not find any degenerated fibres descending into the cord in a case of nearly complete destruction of the mesencephalic tegmentum. In this case a tumor which had existed for a year had caused complete degeneration of descending systems such as the central tegmental tract, but no degeneration was present at the site attributed to the rubrospinal tract. Other investigators however, maintained that they could find degenerated rubrospinal fibres in man. (Stern (1938), Holmes (1904), Collier and Buzzard (1901), Dimitri.)

The spinocerebellar tracts.

Collier and Buzzard in 1903 gave an exellent description of both spinocerebellar tracts which were found to be degenerated after spinal cord lesions at different levels. They studied 12 cases and located degenerated fibres under the pia over the whole extent of the lateral funiculus. The areas of the dorsal and the ventral spinocerebellar tract stood out as central bulgings of this peripheral band of degenerated fibres. The dorsal spinocerebellar tract was situated mainly in the dorsal tip of the posterolateral funiculus and the ventral spinocerebellar tract in a triangular area in the periphery of the anterolateral funiculus. In the area of the ventral spinocerebellar tract the investigators also located the spinotectal and spinothalamic fibres. They demonstrated that spinocerebellar fibres terminate not only in the cerebellum, but also in the brain stem and that part of the fibres of the ventral spinocerebellar tract join the dorsal tract in a pontine level. Strong, endeavouring to settle the problem of the possible presence of crossed fibres in the dorsal spinocerebellar tract. studied sections through the lower thoracic segments of the human cord (1936). He clearly demonstrated that fibres leave the column of Clarke only from the ventral and medial

side and immediately turn laterally to enter the homolateral posterolateral funiculus, where they assemble ventral to the pyramidal area. He did not see any fibres crossing in the anterior white commissure. The afferent fibres to the dorsal horn leave the posterior funiculus in a place where fibres, mostly of caudal segments, are present.

The spinothalamic tract.

Another problem in the central nervous system is formed by the spinothalamic connections which have been the subject of many experiments and observations since Spiller introduced anterolateral chordotomy against intractable pain.

In 1932 Foerster and Gagel published the results of a detailed study of their material concerning anterolateral chordotomies. They believed a rigourous systematization to be present in the spinothalamic pathway. From the ventral border of the posterolateral funiculus onward in a ventromedial direction to the anterior medial fissure, fibres conveying temperature, pain and pressure sensations respectively are present. The fibres of different segments are located in concentric lamellas, those from distal segments peripheral and those from the most rostral ones surrounding the grey matter. They admit that many fibres terminate in the reticular substance, but they also find fibres going to the cerebellum, the superior colliculus and the thalamus.

Hyndman and Van Epps, in 1939, localized the spinothalamic fibres as a tract in the anterolateral funiculus underneath the pia mater. They accepted a segmental localization in the tract. Based upon physiological experiments it appeared that the fibres had to be rather thin. It has, however, always been very difficult to demonstrate these fibres anatomically. Ascending degeneration often has been observed in the anterolateral funiculus with the Marchi technique. Initially this degeneration was believed to be in the spinothalamic tract, but afterwards many of these fibres appeared to be spinocerebellar ones.

Walker localized spinothalamic fibres all over the anterolateral funiculus and the lateral part of the anterior funiculus. He found an indication of segmental localization in this system, the sacral fibres lying dorsolaterally, the cervical ones ventromedially, and the remaining fibres in a more or less parallel segmental arrangement. The fibres, conveying thermal sensations, were found in the so-called lateral spinothalamic tract and the fibres conveying some sort of touch sensation in the so-called ventral spinothalamic tract. The pain fibres were present in both tracts, as well as between them. Walker stated that the number of degenerated fibres in the spinal cord considerably outnumbers the fibres terminating in the thalamus (Walker 1940). Possibly, the tract is interrupted by one or more synapses and for this reason some investigators speak about a spino-reticulo-thalamic tract. It is generally accepted that the spinothalamic fibres arise in the nucleus of the dorsal horn and within 1—2 segments cross in the anterior white commissure. In the anterolateral funiculus there is always a considerable intermingling with the fibres of the ventral spinocerebellar and the spinotectal tract. The recurrence of pain sensation after complete anterolateral chordotomy points to an even wider distribution of spinothalamic fibres over the cross-section of the spinal white matter. (Walker 1943, Gardner and Cuneo, 1945.) It is not possible to differentiate at a spinal level between the spinocerebellar, spinotectal and spinothalamic fibres. (Rasmussen and Peyton, 1941; Schwartz and O'Leary, 1942; Walker.)

Guillaume localizes the spinothalamic fibres in the anterior and anterolateral funiculus with a more dorsoventrally orientated lamellation of segments than was assumed by Walker (1948).

White, after discussing the problem several times, came to the conclusion that the pain fibres are certainly not situated in a small fibretract underneath the pia in the anterolateral funiculus, as was accepted by Gray, Ranson and Riley.

THE MONKEY'S CORD.

An atlas of the monkey's cord does not exist. Both in Geist's paper on the brain of macaca mulatta (1930) and in Monnier's atlas, only the transition of the medulla and the cord are described and pictured.

Verhaart, in 1954, described the fibre structure of the anterior and the lateral funiculus as seen in Häggqvist-stained slides. The majority of the tracts showed a typical fibrepattern only in the high cervical cord. In lower levels admixture of fibres of different pathways proved to be very common.

In the high cervical cord the lateral pyramidal and the dorsal spinocerebellar tract fill the posterolateral funiculus. In its lateral half they were greatly intermingled but in the medial half pyramidal fibres prevailed. The rubrospinal tract was located closely ventral to them, in a triangular area situated at the transition of the postero- and the anterolateral funiculus. Lateroventral to the rubrospinal tract, along the margin of the anterolateral funiculus, the ventral spinocerebellar tract was found in a triangular area.

Along the ventromedial fissure a small strand of pyramidal fibres was found, and lateral to it the continuation of the medial longitudinal fascicle. Along the ventral margin of the anterior funiculus, Deiters' vestibulospinal tract could be distinguished. Downward into the thoracic cord all tracts diminish in size and the dorsal spinocerebellar and the lateral pyramidal tract were no longer intermingled. Both the ventral spinocerebellar and the rubrospinal tract could no longer be distinguished, as such, in a midthoracic level, although rubrospinal fibres were mixed with pyramidal ones. In the lumbar segments the only tracts to be recognized were the lateral pyramidal tract and the medial longitudinal fascicle. The area in which no separate tracts were found had increased greatly in size, relative to the whole surface area of the anterior and the lateral funiculi. *A circumscribed spinothalamic tract could not be found;* spinothalamic fibres were assumed to occur mixed with other ones within the anterolateral funiculus.

Papers in which studies of certain tracts in the cord were described will now be recorded.

The pyramidal tract.

The location of the lateral corticospinal tract is fairly well established in the monkey and occupies most of the postero-lateral funiculus.

Fulton and Sheehan, in 1935, described that ten per-cent of the pyramidal fibres do not decussate but go to the homolateral pyramidal tract in the cord. The ipsilateral ventral pyramidal tract can be followed down to the lower thoracic segments. This confirms what was already published on this subject from animal experiments and human pathology.

In the same year Kennard and Hoff demonstrated that a considerable number of pyramidal fibres arose in the pre-motor cortex. These fibres travel with the motor pyramidal fibres but are not present in the ventral tract. The quantitative relations between crossed and uncrossed fibres is 4:1. The promotor pyramidal fibres terminate, as do the motor ones, in the intermediate grey substance at the base of posterior and anterior horn. Some fibres terminate on small cells in the anterior horn.

In 1938, Levin and Bradford reported that twenty percent of the pyramidal fibres in the macaca monkey arise, outside Brodmann's area 4, in the sensory and the parietal cortex. Eighty-five percent of the pyramidal fibres crossed at a spinal level to form the lateral pyramidal tract.

Lassek, who performed many experiments on the pyramidal system, stated in 1943, that the pyramidal tract in the monkey contains approximately 500,000 fibres with diameters ranging from one to twelve μ, the thin fibres being most abundant. Only two percent of these fibres can be derived from Betz' cells in the motor cortex. He was not able to find a correlation between the degree of motor skill of the different extremities and the localization of cells in the motor cortex, when comparing Ateles and Macaca monkeys with man.

In 1944 Welch and Kennard found that the pyramid showed only a moderate degree of degeneration after ablation of areas 4 and 6, but that degeneration was nearly complete after a total decortication. In the spinal pyramidal tract, however, many fibres were preserved. Thus they concluded that many subcortical extrapyramidal fibres must be present in the pyramidal tract in the lower brainstem and spinal cord.

In 1945 Gobbel and Liles demonstrated the presence of corticofugal fibres, descending with the pyramidal tract to the cervical cord, originating from the parietal cortex.

Brookhart and Morris found in 1948 that the pyramidal tract contains fibres of all diameters between 1 and 12.5 μ. Most of the fibres possessed a diameter between 3 and 6 μ. They tried to correlate these diameters with the recorded conduction velocities. This conduction velocity ranged between 164 to 1.8 meter per second. Most of the fibres however, possessed a conduction velocity between 35 and 60 meters per second. From these conduction velocities it also follows that fibres with a large range of diameters must be present in the pyramidal tract of the cat. They were able to demonstrate physiologically that pyramidal fibres descended to the sixth lumbar segment. The greater part of the pyramidal fibres, however, terminated in the cervical intumescence.

In 1952, Lassek came to similar conclusions. After cortical ablations one third of the axons, mainly thin ones, was always preserved.

Mettler, in 1944, found that the corticospinal tract nearly completely crosses in the monkey and that the fibres are dispersed through the posterolateral funiculus of the cord. In some cases he could not find any corticospinal fibre in the ventral funiculus. Homolateral fibres were present, however, in the lateral tract. The degenerated fibres could be followed caudally to sacral segments.

Other descending systems.

In the same paper Mettler described the degeneration of the rubrospinal system (1944). He found its fibres

assembled in a conspicuous tract in the brainstem, the tract being composed of fibres twice as thick as those of the pyramidal tract. The fibres keep together in the spinal cord and are situated just ventral to a line dividing the lateral funiculus into a dorsal and a ventral half. In the cervical enlargement, however, the rubrospinal fibres gradually become dispersed and in the uppermost thoracic levels occupy the intermediate part of the lateral funiculus. They can be followed caudally to lumbar levels.

Of the vestibulospinal system Mettler stated that the lateral vestibulospinal tract contained mainly uncrossed fibres, together with a number of crossed ones. This tract fuses with the fibres of the medial longitudinal fascicle in the spinal cord. The medial longitudinal fascicle, according to him, contained crossed as well as uncrossed vestibulospinal fibres. The fibres of the medial reticulospinal tract were also enclosed in the medial longitudinal fascicle. Lateral reticulospinal fibres were present in the lateral vestibulospinal tract.

The ventral spinocerebellar tract.

An excellent description of the ventral as well as the dorsal spinocerebellar tract was given by Mott in 1892 in an experimental study on the monkey. He entirely confirmed the observations of Löwenthal in the cat, on the course of the ventral spinocerebellar tract. He was disinclined to accept the presence of pain-conveying fibres in the anterolateral funiculus.

In 1940 Cooper and Sherrington found chromatolysis of ganglion cells in the ventral horns between the twelfth thoracic and the seventh lumbar segment following cervical chordotomy in Macaca monkeys. In a hemichordotomy chromatolysis was contralateral. The cells lay peripherally in the grey matter and were called "border cells". Morphologically they resembled the myorhabdotic cells of the ventral horn. Authors were convinced that the axons of these cells formed the ventral spinocerebellar tract.

In the above cited paper of Mettler (1944) the author

confirmed these results. He even found retrograde degeneration of seemingly motor cells in the ventral horn of the cervical enlargement after a cerebellar ablation. In the spider monkey he was able to find these border cells in the sacral cord.

Sprague also confirmed these results (1950, 1951). He counted the number of the border cells and was able to distinguish them from the myorhabdotic cells; six to twenty percent of the ventral horn neurons proved to belong to them. He demonstrated that at least part of their axons terminate in the cerebellum.

In the same year, Morin performed similar experiments. He agreed with the retrograde cell degeneration in the lumbar anterior horn after hemichordotomy, but could not find it after severance of the superior cerebellar peduncle. He therefore concluded that the axons of the border cells do not travel in the ventral spinocerebellar tract, but that these cells give rise to a propriospinal tract, connecting lumbar with cervical segments.

In 1949 Chang and Ruch found fibres in the ventral spinocerebellar tract of the spider monkey, which ascend to the diencephalon and cross in the ventral supraoptic commissure. They were not able to demonstrate these fibres in the cat.

In 1953, Yoss, using Marchi's technique, studied ascending degeneration in the spinal cord of the monkey after hemichordotomies at various levels. According to him the ventral spinocerebellar tract is situated in the anterolateral funiculus just underneath the pia mater and stretches out ventrally into the anterior funiculus. The distal segments are located dorsolaterally in the tract, the proximal segments medially. The majority of the fibres arise in the caudal segments. Spinothalamic fibres have the same distribution but lie more centrally and have a smaller diameter.

The dorsal spinocerebellar tract.

It is generally agreed that the dorsal spinocerebellar fibres have their origin in the homolateral column of Clarke. In 1951 however, Chang demonstrated dorsal spinocerebellar

fibres in the spider monkey, which arise in segments caudal to the column of Clarke, which has its caudal limit at L_2. He was able to demonstrate that the cells of origin were situated medially in the intermediate horn. Although there were also degenerated fibres in Gowers' area, no chromatolysis was found in the ventral grey column of the caudal segments.

In 1952 Yoss published a paper about the dorsal spinocerebellar tract in the monkey. No fibres arise from segments caudal to L_3 but many arise from the first two lumbar segments and the caudal thoracic segments. In the twelfth thoracic segment those fibres are situated somewhere between the lateral pyramidal tract and the intermediate horn. In more proximal segments dorsal spinocerebellar fibres take a more peripheral course in the posterolateral funiculus. The caudal segments are located dorsomedially in the tract, the proximal segments ventrolaterally. Hardly any fibres join the spinocerebellar tract between C_4 and Th_4 segments.

The spinothalamic tract.

After Edinger, in 1889, indicated the existence of spinothalamic connections in man, Spiller, in 1905, discovered that pain and temperature sensations were conducted to the thalamus by fibres situated in the anterolateral funiculus of the cord. Many papers concerning the site of these fibres have appeared since, and a general agreement was reached about their crossing at the level of origin and their ascent to the thalamus. Segmental arrangement was suggested by Walker, Hyndman and Van Epps (1939).

Weaver and Walker, in 1941, made systematic chordotomies in order to study this arrangement. Marchi-technique showed peripheral degeneration in the anterolateral funiculus, but segmental arrangement was not obvious in the cord. In the brain stem however, it could more or less be demonstrated.

Chang and Ruch, in 1947, pointed out that ascending degeneration is not abundant in the cat, whereas in the monkey a clearcut spinothalamic tract could be found only in the

mesencephalon. Segmental localization however, was thought to be the case.

Morin and O'Leary, in 1950 approved of Weaver and Walker's conclusions. They stressed the close topical relationship between the spinothalamic and the ventral spinocerebellar tracts. Besides spinothalamic fibres they saw spinoreticular fibres, ascending from a lesion in the cord. Chromatolysis in cases of severance of the anterolateral funiculus was located in the ventral border cells of the lumbar segments.

Morin, Schwartz and O'Leary in 1951, found one bundle of degenerating fibres, following severance of the anterolateral funiculus in monkeys, which they assumed to consist of spinothalamic, spinoreticular, spinotectal and spinocerebellar fibres. In their Marchi preparations they could not differentiate those fibres. They stated that in the medulla some of the spinothalamic fibres were found to lie dorsal to the inferior olive.

Yoss, in 1950, described a spinothalamic tract, mediating deep sensation, with the same localization as the ventral spinocerebellar tract.

In 1938 Blakeslee, Freiman and Barrera described the lateral reticular nucleus in the medulla of the monkey. They found that all its efferent fibres proceeded to the cerebellum, whereas its afferent fibres came from the lateral funiculus of the cord. Some fibres of the spinocerebellar tracts gave off collaterals to the nucleus. The afferent fibres to the nucleus were situated in the lateral funiculus medial to the spinocerebellar fibres and they were scattered among other fibres.

Propriospinal fibres.

In 1941, Tower, Bodian and Howe found propriospinal fibres to be located centrally in the white matter, bordering the ventral and intermediate horns at all sides. They were mainly of small sizes and many of them arose from small cells in the ventral horn. Preserved fibres, however, were also present in the periphery of the isolated spinal cord segments.

Even thick fibres were preserved and were situated at two places viz: the reticular area between the dorsal and ventral horn and the dorsal part of the anterior funiculus where they are in relation with the anterior white commissure.

Sprague in 1951, came to about the same results.

THE CAT'S CORD.

Winkler and Potter, in 1914, described only a cross-section of the transition of the medulla and the cord, and of the first cervical segment in their atlas on the cats brain. They distinguished a posterior (medial) longitudinal fascicle along the anterior medial fissure and lateral to it a predorsal fascicle. Along the ventral margin of the anterior and the anterolateral funiculus they located the vestibulospinal tract, and along the lateral margin of the lateral funiculus both spinocerebellar tracts. The spinothalamic tract in their pictures was found medial to the dorsal part of the dorsal spinocerebellar tract in the caudal medullary level, the rubrospinal tract medial to the spinothalamic tract and the lateral pyramidal tract medial to the rubrospinal tract. Each of the four tracts, therefore, is found within the posterolateral funiculus. They considered the anterior pyramidal tract as nonexistent in the cat.

In 1949 Monnier, published his atlas of the brain stem of the cat and the monkey. He gave only a picture of a myelin-stained transverse section of the first cervical segment of the cord. In this section the following tracts were located. In the lateral funiculus were put successively from ventral to dorsal: the spinothalamic tract, the rubrospinal tract, the lateral reticulospinal tract and the lateral pyramidal tract. The ventral and the dorsal spinocerebellar tracts were located along the lateral border of the lateral funiculus. Along the medial ventral fissure were located the ventral pyramidal tract and the tectospinal tract lateral to it. Finally, the vestibulospinal tract was localized ventral to the anterior horn, as was the medial reticulospinal tract.

In a recent publication (1953) Verhaart published the first results of a fibre analysis of the anterior and lateral

funiculus of the cat's cord. In this study the topography of the tracts at various levels was compared, and did not prove to be essentially changed. The only changes were the ending of short tracts and the decrease in size of the longer tracts in their downward course, with the resulting shift of the tracts to a more peripheral place.

In a high cervical level, the medial longitudinal fascicle is situated along the anterior medial fissure with a slight lateral extension along the ventral border of the anterior funiculus. The vestibulospinal tract is located more or less in continuation with this extension along the ventral margin of the anterior funiculus, its lateral tip encroaching upon the anterolateral funiculus. The lateral pyramidal tract occupies the centre of the posterolateral funiculus, medially bordering the posterior horn. Ventrolateral to it the rubrospinal tract is located in a large triangular area. The dorsal spinocerebellar tract lies underneath the pia mater from the posterior horn laterally. The ventral spinocerebellar tract is visible as a small area ventral to the rubrospinal tract underneath the pia mater in the anterolateral funiculus.

When followed downwards these tracts become smaller. The dorsal spinocerebellar tract, the lateral pyramidal tract, the rubrospinal tract and the ventral spinocerebellar tract keep together and their combined area lies finally within the posterolateral funiculus. Except for the decrease in size, no changes occur in the location of the medial longitudinal fascicle and the vestibulospinal tract. The ventral spinocerebellar tract has disappeared, as such, at a midthoracic level. In the lumbar and sacral segments only the dorsal spinocerebellar, the lateral pyramidal and the rubrospinal tract can be identified as small areas with a typical fibrepattern. A ventral pyramidal tract could not be found in the cat. Demarcation of tracts becomes more and more difficult in the lower parts of the cord.

In a paper in 1942, Szentagothai-Schimert followed the descending systems in the spinal cord and especially paid attention to the site of their terminals. The pyramidal tract ended around cells at the base of the posterior horn and

the intermediate horn. The rubrospinal tract was found to terminate at the contralateral side at the same place, in cervical and lumbar segments. Its terminals were placed more medially than those of the pyramidal tract. Only the contralateral tectospinal tract could be followed and was found to descend to the upper thoracic segments, where it terminated in the medial part of the ventral posterior horn cells. The vestibulospinal tract, however, appeared to terminate around the cells in the ventral horn, which innervate the long muscles of back and neck. The medial longitudinal fascicle, which contains many fibres from the nucleus of Deiters, was severed in a level rostral to the vestibular complex. No terminal degeneration could be found in the anterior horn.

In 1932, in a study on hypertonus following spinal cord lesions, Ranson, Muir and Zeiss also produced the pictures of the descending degeneration in the cervical cord. The lateral pyramidal tract was located centrally in the posterolateral funiculus, the rubrospinal tract just ventral and lateral to it. The vestibulospinal tract appeared to be situated quite peripherally in the transitional area of the anterior and the anterolateral funiculus. This tract was continuous with the medial longitudinal fascicle in the ventral funiculus.

No other complete survey of the hodology of the cord of the cat is available as far as I know. As for the separate tracts the more recent publications are of more importance and only these will be reported.

The pyramidal tract.

In 1932 McKibben and Wheelis performed experiments on the motor cortex of the cat and found a topical organisation in the cortex. Following ablation of parts of the motor cortex they found degeneration of the lateral pyramidal tract, situated in the centre of the posterolateral funiculus. In the lateral pyramidal tract no topical organisation was to be distinguished. Many fibres were preserved, even after a complete motor cortex ablation. The tract could be followed caudally to lumbar segments.

In the course of investigations on motor disturbances after brain stem lesions, Mettler and Zimmerman in 1943, also made several remarks about long descending systems of the spinal cord. They located the lateral pyramidal tract in the medial part of the posterolateral funiculus. No uncrossed ventral pyramidal tract was found.

In 1953, Walberg and Brodal described the presence of fibres in the lateral as well as in the ventral pyramidal tract of the cat, having their origin not in the frontal motor cortex but in the temporal as well as in the occipital lobe of the cerebrum. Even in the homolateral pyramidal tract those fibres were present. This, according to their opinion, can only be explained by a first crossing in the corpus callosum, which they were able to find

In 1954, Lance stated that there were no unmyelinated fibres in the pyramidal tract and that no pyramidal fibres occurred below the fourth lumbar segment. According to him no fibres leave the tract between the third thoracic and the first lumbar segment. He was unable to find a ventral pyramidal tract. All the pyramidal fibres in the spinal cord were crossed.

Other descending systems.

Papez, in 1926, described three reticulospinal tracts in the cat, a medial one in the anterior funiculus between the medial longitudinal fascicle and the ventral fasciculus proprius, a lateral one between the lateral pyramidal tract and the rubrospinal tract, and a ventral one in the anterior funiculus dorsal to the vestibulospinal tract.

In 1932 Allen published a paper dealing with the reticular substance. In this paper he described several afferent systems to the reticular formation: tectobulbar fibres and fibres from the fastigial nucleus of the cerebellum and the vestibular nucleus, travelling via the medial longitudinal fascicle. Allen approved of the existence of a lateral and a reticulospinal pathway concerned with vascular and respiratory functions. He did not accept that similar functions were mediated by

the rubrospinal, the pyramidal or the tectospinal tracts. He was disinclined to accept the existence of fibres from the solitary nucleus descending in the lateral funiculus of the cord.

In 1947 Niemer and Magoun found with physiological experimentation that the reticulospinal pathways were very diffuse in the lateral and ventral funiculus of the cord. Even a functional differentiation between these fibres proved to be very difficult. Crossed and uncrossed fibres were equally present. They, therefore, disagree completely with Papez.

In 1926 Gray published the results of an extensive study of the vestibular system. He reported that the medial longitudinal fascicle only contained crossed vestibulospinal fibres, which arise mainly from the descending nucleus and to some extent from the medial nucleus. The lateral nucleus gives rise to the homolateral vestibulospinal tract. The homolateral fibres, possibly present in the medial longitudinal fascicle and descending into the cord, were considered to be of reticular origin. In his diagrams he also indicated the rubrospinal tract and the reticulospinal tracts found by Papez.

In 1932, Rasmussen gave an extensive paper on the secondary vestibular tracts. He found that the descending vestibular tracts were organized as follows. The medial longitudinal fascicle contained, in its homolateral component, fibres from the superior vestibular nucleus and also some from the medial and the descending nucleus. Possibly some fibres of the lateral vestibular nucleus were enclosed in it. The contralateral medial longitudinal fascicle contained mostly fibres from the medial and the descending nucleus of the vestibular complex. The lateral vestibular nucleus gave rise to the lateral vestibulospinal tract of Deiters which also might contain some crossed fibres.

In 1937, Buchanan repeated the experiments on the vestibular system with the following results. The medial nucleus was the origin of homo- and contralateral fibres in the medial longitudinal fascicle, descending into the cord to the thoracic segments. The superior nucleus gave off some homolateral descending fibres in the medial longitudinal fas-

cicle and the descending nucleus both homolateral and contralateral fibres to this fascicle. The latter fibres, however, are small in number. According to the author the lateral vestibular nucleus gave not only rise to the uncrossed vestibulospinal tract, but also to homolateral fibres in the medial longitudinal fascicle descending to all cord segments and to contralateral fibres in the same fascicle, not descending below the cervical segments.

Already in 1901 van Gehuchten had pointed to the intimate relationship between the rubrospinal tract and the ventral spinocerebellar tracts. In his study on rabbits and dogs he pictured these tracts in the brain stem and cord in the lateral funiculus. That close relationship has been the cause of many mistakes whereby both tracts were taken for each other. Van Gehuchten denied the existence of uncrossed pyramidal fibres in these animals.

In the above quoted article of Mettler et al. (1943), the rubrospinal tract was pictured just ventrolateral to the area occupied by the pyramidal tract. The authors approved of the reticulospinal tracts described by Papez, and especially pictured the medial reticulospinal tract. The authors did not accept the existence of a lateral uncrossed reticulospinal tract.

In 1935 Rasmussen published the results of his investigations on the tectospinal system. These fibres appeared to be completely crossed in mesencephalic level. The fibres arose only from the superior colloculus. Part of the fibres terminated in the pons and reticular substance, but many fibres could be followed caudally into the spinal cord, where they lay dispersed throughout the medial longitudinal fascicle. They could not be found caudal to the seventh cervical segment.

In 1952, Bucher and Bürgi found long descending fibres in the medial longitudinal fascicle of the cat, which have their origin in the interstitial nucleus of Cajal.

The spinocerebellar systems.

In a recent paper on the cerebellar inflow (1953), Carrea and Grundfest studied the ventral spinocerebellar tract

and gave the following survey of older literature. According to them Bastian was the first to describe ascending degeneration in the ventrolateral region of the spinal cord of man, which he called a part of the "cerebellar tract" (1867). At that time the name of Gowers was attached to the "anterolateral ascending tract", which was known to be connected with the contralateral posterior roots. Gowers, however, denied the existence of a long ascending anterolateral tract to the cerebellum. Löwenthal, in 1885, was the first to describe the ventral spinocerebellar tract throughout its course, entering the cerebellum via the superior peduncle. Two years later, Singer found chromatolysis of anterior horn cells when this tract degenerated following a lesion of the thoracic cord. For these reasons, Carrea and Grundfest *propose that the ventral spinocerebellar tract should be called after* Löwenthal *and* Singer *instead of* Gowers.

Auerbach (1890) was one of the first to give a detailed description of the degenerated ascending fibres in the cord of the cat, following hemisection of the cord. The tract of Flechsig was found to be homolateral and to be located dorsally in the posterolateral funiculus. The ventral spinocerebellar tract showed degeneration even after section of the lumbar cord, which was not the case with the dorsal spinocerebellar tract. The author also found contralateral degeneration dorsal to the inferior olive, even after section of the cord in low levels. In levels rostral to the medulla this degeneration could no longer be found.

In 1910 Bruce found that ventral spinocerebellar fibres arose from the caudal extremity of the ipsilateral column of Clarke. She also saw ventral spinocerebellar fibres penetrate into the dorsal tract. From this she concluded that there was no essential difference between the dorsal and the ventral spinocerebellar tract.

Beck, in 1927, published a paper in which he described dorsal spinocerebellar fibres *which arise from as low a segment as the second sacral.* He was only able to distinguish a clearcut ventral spinocerebellar tract at the first lumbar segment. The

fibre density was much greater in the dorsal than in the ventral spinocerebellar tract. He observed the presence of ascending fibres between both spinocerebellar tracts and gave them the name of "tractus spinocerebellaris intermedius". He saw these fibres enter the restiform body, after they passed through the lateral reticular nucleus. This is contrary to the view held by Pellizi. Beck could not find any fibres from a spinal level, ascending rostral to the point where the ventral spinocerebellar tract shifts dorsally to enter the cerebellum along the dorsal border of the brachium conjunctivum. He described that the spinocerebellar tracts consisted only of homolateral fibres.

Pass, in 1923, wrote that no dorsal spinocerebellar fibres arise caudal to the caudal extremity of the column of Clarke in the cat. He injected a silvernitrate solution into the grey matter of the cord and also performed midline incisions. His results led him to the conclusions that nearly all dorsal spinocerebellar fibres cross after their origin from Clarke's column. He also said that the fibres of the ventral spinocerebellar tract cross via the dorsal grey commissure. He considered the nucleus cuneatus externus to be the cervical homologon of the column of Clarke. All primary afferent fibres from segments lower than L_2 terminated in the caudal extremity of Clarke's column.

In 1942, Grundfest and Campbell found that the dorsal spinocerebellar tract in the cat consisted for the greater part of very thick fibres. The fibres arise from Clarke's column which descends to approximately the third lumbar segment. They were not able to demonstrate clearly the presence of crossed fibres in the tract. The tract was only activated by afferent muscle impulses.

In 1950 Lloyd and McIntyre, by means of electric stimulation of afferent fibres of hindleg muscles, showed that impulses, after entering the spinal cord at the first lumbar segment, have a one to one relay with the cells of Clarke's column. The second neuron axons appeared to be located in the dorsal spinocerebellar tract.

Morin and Hadded, in 1953, by a similar method, proved that both the dorsal and the ventral spinocerebellar tracts contain crossed as well as uncrossed fibres. When both the dorsal funiculi and spinocerebellar tracts are interrupted, afferent muscle as well as cutaneous impulses still reach the cerebellum. For this reason they thought it probable that spino-olivo-cerebellar and spino-reticulo-cerebellar connections exist. In the monkey they proved the same facts.

Sprague, in 1953, demonstrated the existence and location in the cat of the so called "border cells" in the lumbar ventral horns, found by Cooper and Sherrington in the monkey. Their axons lie in the anterolateral funiculus near the grey matter. Activation of these cells produces effects different from those following activation of the dorsal spinocerebellar tract.

In 1954, Carrea and Grundfest published the results of an elaborate physiologic investigation of the ventral spinocerebellar tract. The fibres arise both in the lumbar ventral horn and in the cervical cord from ill-defined cells. All lumbar fibres cross but from the cervical fibres, only fifty percent crosses. Sensory qualities are mediated by this tract and impulses are conducted at a rate ranging from 30 to 80 M/sec. The tract is not pure in the cord and its fibre diameter ranges from 5 to 14 μ.

The spinothalamic tract.

In 1914, Karplus and Kreidl found that painful sensations were transmitted to higher levels even after hemisections of the cord at a cervical and contralateral thoracic level. From this they concluded that the grey matter is most important for the transmission of painful sensations to higher levels. They were not able to demonstrate the same phenomenon in monkeys.

In 1950, Berry, Karl and Hinsey were able to differentiate spinothalamic fibres from medial lemniscal and spinocerebellar fibres, lateral to the inferior olive.

In 1952, Aidar showed the existence of fibres, situated in

the anterolateral funiculus, which mediate slow impulses coming from the splanchnic nerves.

Gardner and Haddad, in 1953, on the contrary, came to the conclusion that spinothalamic fibres do not occur in the cat. Afferent sensory impulses from the hindlegs reach the higher centres via diffuse, ill-defined pathways. This was confirmed by Morin in the same year, who stated that a large number of fibres ascend diffusely in the cord to end in the reticular substance of the medulla and the higher brain stem, from where fibres ascend farther to the thalamus.

Kennard, in 1954, wrote that she was not able to interrupt the pain conduction in the cat even with a bilateral anterolateral chordotomy. However, when the dorsal half of the cord was severed, pain perception was markedly reduced. From this she concluded that the majority of the pain fibres are situated in the posterolateral funiculus in the cat and possibly in the dorsal funiculus. This was confirmed to some extend by anatomical experiments.

Other ascending tracts.

In 1949, Brodal described fibres, going from the cord to the lateral reticular nucleus in the medulla. They came from segments as low as lumbar, but their site in the cord could not be determined with certitude.

Brodal, Walberg and Blackstad in 1950 described spino-olivary fibres in the cat, many of which having their origin in the lumbosacral region. These fibres were located in the anterior funiculus.

In 1954, Grundfest and Carter found, by physiological means, that the inferior olive could be activated by peripheral stimulation even when only the posterolateral funiculus of the cord was intact. With partial chordotomies they demonstrated the existence of homolateral fibres which cross diffusely between the third and first cervical segment and, on the opposite side, assume a ventral course. This dorsal spino-olivary tract is already present in lumbar levels. Its fibres conduct afferent impulses from the skin.

Recently (1955), Grundfest and Biagio found that the nucleus of origin of the spino-olivary tract, described by Grundfest and Carter, was situated at approximately L_5. There were no afferents from the trunc to the tract and afferents from the fore limb were not investigated upon. The fibres of the spino-olivary tract must be of intermediate size, for their conduction velocity was 63 M/sec. The nucleus of origin could not be the column of Clarke, but was situated in the posterior horn.

From 1951 to 1953, combined studies of Brodal and Rexed led to the discovery of a nucleus in the cervical cord of the cat, which sends its axons to the cerebellum of the opposite side. Afferent fibres to this lateral cervical nucleus proved to originate from all levels of the cord and from both sides. They were located in the posterolateral funiculus, near the dorsal spinocerebellar tract, though they were not identical with this tract.

In 1952, Brodal and Walberg described ascending fibres in the pyramidal tract of the cat. After a chordotomy, ascending degeneration was present, on both sides, in the posterolateral as well as in the anterior funiculus. The fibres arose from all levels of the cord and could be followed rostrally to the cerebral cortex.

In the next year they proved that part of these fibres terminate in the pontine nuclei. The number of the ascending fibres in the pyramidal system did not exceed four percent of the total number of fibres present. The termination in the pontine nuclei might be established by collaterals.

CHAPTER 3.

EXPERIMENTS.

Experiments were carried out in order to add to and control the data derived from normal specimens. In total 36 cats were used. Hemichordotomies were performed on 11 cats. Most of the chordotomies were at one level, but a few were at two different levels of the same side. In 4 cats a complete chordotomy was done, two of them at the cervical, the others at the lumbar cord. A sagittal splitting of the cord was done at a midcervical and at a high thoracic level. In 9 cases lesions of the medulla were made: two of these were concomitant to a total cerebellar ablation, two others were made in an attempt to sever the internal arcuate fibres and in the remaining ones there was the intention to make a lesion in some nucleus of the medulla. In 4 cats partial or total severance of one half of the midbrain was performed and finally the superior colliculus was ablated in two cats. Five cats underwent partial or total ablation of one half or the cerebrum. Survival periods after operation varied from one week op to four months in order to be able to follow the degenerating fibres after a relatively short period, and to analyse the quantity of preserved fibres after a long survival period. Details will be described with the experiments.

The cord of the cat shows hardly any sign of an ascensus medullae, the spinal cone lies between the first and second sacral vertebra. The segmental subdivision is as follows: 8 cervical, 13 thoracic, 7 lumbar, 5 sacral segments, and 3 coccygeal ones.

DESCRIPTION OF THE EXPERIMENTS.

Cat II 536, right sided hemispherectomy, was sacrificed after 7 months. Only part of the lentiform nucleus was spared. As a result the left lateral pyramidal tract was nearly completely degenerated in the cord.

Cat H 539, right sided hemispherectomy, was sacrificed after 75 days. Resultant degeneration of the right pyramidal tract.

Cat H 542, left sided hemichordotomy at C_2 segment, died after 8 days. The lesion was complete at the left side except for part of the left posterior funiculus.

Cat H 544, left sided hemichordotomy at C_3 segment, was sacrificed after 42 days. The lesion severed the left side of the cord completely except for a small part of the posterior funiculus. It extended across the medial plane into the right anterior funiculus.

Cat H 2505, ablation of the left superior colliculus, was sacrificed after 21 days. The lesion was fairly complete and the corpus callosum was divided.

Cat H 2544, left sided hemichordotomy at C_7 segment, was sacrificed after 83 days. The lesion was complete at the left side, and besides this it severed the most dorsal tip of the right posterior funiculus. At the side of the lesion a scar of connective tissue, neuroglial tissue and small cystes were found No axons traversed the scar.

Cat H 2546, left sided hemichordotomy between C_7 and C_8 segment, was sacrificed after 16 days. The lesion extended across the medial plane into the right anterior and posterior funiculus. A frontal ablation was carried out at the same time as the chordotomy, with resultant pyramidal degeneration.

Cat H 2560, left sided hemichordotomy at L_1 segment, was sacrificed after 21 days. The chordotomy extended far into the right half so as to make the chordotomy almost total. The left side of the cord was completely sectioned.

Cat H 2561, left sided chordotomy at Th_{12} segment, was sacrificed after 21 days. The left half of the cord was completely severed, together with the grey matter of the right half.

Cat H 2570, ablation of the cerebellum, was sacrificed after 51 days. This ablation was accompanied by considerable damage of the medulla, especially the lateral and descending vestibular nuclei of the right side. The left tectospinal tract was also degenerated.

Cat H 2572, left sided hemichordotomy at S_1 segment, was

sacrificed after 30 days. The whole left half, together with both posterior funiculi, was severed. The medial part of the anterior funiculus and part of the grey matter of the right half were also involved.

Cat H 2591, ablation of the cerebellum, was sacrificed after 25 days. The right inferior colliculus was severed and a large necrotic area was found in the tegmentum underneath it, which comprised the lateral part of the right cerebral peduncle. At the same side the vestibular nuclear complex, the lateral lemniscus, and part of the descending branch of the trigeminal nerve were destroyed. Also the rostral part of the dorsal funicular nuclei was destroyed together with the dorsal nucleus of the vagal nerve. The resulting degeneration consisted of the right vestibulospinal tract, the left lateral pyramidal tract and the tectospinal fibres. The medial longitudinal fascicle also contained many degenerated vestibulospinal fibres.

Cat H 2601, midline splitting of the cord at the 4th thoracic segment, was sacrificed after 22 days. The medial parts of the anterior and posterior funiculi were damaged together with the base of the posterior horns and Clarke's column.

Cat H 2635, a lesion of the left half of the mesencephalon which appeared to sever only the cerebral peduncle, was sacrificed after 28 days. Resulting degeneration of the right lateral pyramidal tract in the cord was observed.

Cat H 2637, severance of the internal arcuate fibres, was sacrificed after 25 days. The lesion, because of hemorrhage, extended into the lateral and dorsomedial part of the reticular substance. The lesion was at a caudal level of the medulla and did not interrupt any of the known fibresystems in it. The resulting degeneration was located in the anterolateral area of the cord.

Cat H 2659, severance of the internal arcuate fibres, died after 8 days. The hemorrhage in this case was more extensive than in the previous one and the reticular substance was completely destroyed. The nuclei of the dorsal funiculus were destroyed at the same side. The lesion extended into the pyramidal decussation and destroyed part of the lateral funiculus. The resulting

degeneration was situated in the lateral pyramidal tract, the rubrospinal tract of the left side, and many reticulospinal fibres were degenerated on both sides.

Cat H 2671, lesion of the right nuclei of the dorsal funiculus and the left dentate nucleus, was sacrificed after 21 days. The lesion destroyed only the cuneate nucleus but extended from dorsomedially ventrolaterally to the pia mater, interrupting most of the rubrospinal and internal arcuate fibres, resulting in degeneration in the cord of the right rubrospinal tract and some reticulospinal fibres.

Cat H 2706, double left hemichordotomy at the level of C_4 and C_7 segments, was sacrificed after 24 days. The lower lesion left the posterior and anterior funiculus undamaged. The rostral lesion was more complete but spared the most medial part of the anterior funiculus.

Cat H 2725, midline splitting of the cord between C_4 and C_7 segment, was sacrificed after 20 days. The medial part of the anterior and posterior funiculi were damaged together with the base of both posterior horns.

Cat H 2729, ablation of the left superior colliculus, was sacrificed after 21 days. The colliculus was removed by suction with slight damage to the dorsal part of the tegmentum and the pulvinar of the thalamus.

Cat H 2748, left hemichordotomy at the level of C_7 segment, was sacrificed after 21 days. This experiment was performed because cat H 2546 survived the operation for only 16 days and in addition had a frontal cortical ablation. The lesion did not extend across the medial plane and spared the anterior funiculus. Unfortunately, this cat had an abnormal tract topography in the cord because of a glial membrane in the lateral funiculus.

Cat H 2751, left hemichordotomy at the level of the 9th thoracic segment, was sacrificed after 22 days. The lesion was somewhat more extensive than in the foregoing case as only the medial part of the anterior funiculus was spared.

Cat H 2760, ablation of the left half of the mesencephalon, was sacrificed after 70 days. The lesion spared the medial quarter of the red nucleus along with the medial longitudinal

fascicle and the third nerve nuclei, but resulted in the degeneration of the contralateral rubrospinal, tectospinal, pyramidal tract and the ipsilateral interstitiospinal tract.

Cat H 2761, chordotomy at the level of C_8 and Th_3 segment, died 13 days after the operation. The lesions were as intended.

Cat H 2800, left sided hemispherectomy, was sacrificed after 56 days. Degeneration of the left pyramidal tract was observed.

Cat H 2804, ablation of the lateral part of the left half of the mesencephalon, was sacrificed after 35 days. The red nucleus was not damaged, but the rubrospinal tract was severed at the transition of the mesencephalon and the pons. The contralateral pyramidal and the tectospinal tract were degenerated in the chord.

Cat H 2807, chordotomy at the level of Th_9, L_1 and L_3 segment, died 11 days after the operation. The upper and lower lesions were not complete. The ventral part of the white matter, ventral to the anterior horn, was spared. The lesion at L_1 was complete.

Cat H 2814, lesion of the lateral part of the medulla, was sacrificed after 26 days. Because of hemorrhage the lesion destroyed the lateral part of the reticular substance, the rubrospinal tract, the descending tract of the trigeminal nerve and the inferior cerebellar peduncle.

Cat H 2816, chordotomy at the level of L_1 and L_4 segment, was sacrificed after 15 days. The lesion at L_4 was not complete since the ventral part of the white matter was spared. The other lesion was complete.

Cat H 2843, lesion of the dorsal part of the reticular substance at the level of the inferior olives, in an attempt to sever the vestibular nuclei which escaped destruction, died after 14 days. The dorsal part of the right medial longitudinal fascicle is interrupted and many reticulospinal fibres are degenerated.

Cat H 2849, ablation of the left frontal cortex, was sacrificed after 23 days. Resulting degeneration of the left pyramidal tract was observed.

Cat H 2855, ablation of the right vestibular nuclear complex, was sacrificed after 105 days. The lesion comprised all cerebellar peduncles, the lateral and medial vestibular nuclei and part of

the superior and descending vestibular nuclei. For no apparent reason the contralateral vestibulospinal tract was also considerably degenerated.

Cat H 2875, left hemichordotomy at the level of Th_4 and Th_7 segment, was sacrificed after 98 days. The lower lesion interrupted the complete left half of the cord and the dorsal part of the posterior funiculus of the right side. The rostral lesion encroached upon the medial part of the anterior funiculus of the right side.

Cat H 2892, hemidecortication at the left side, was sacrificed after 42 days. Resulting degeneration of the right lateral pyramidal tract in the cord was observed.

Cat H 2933, ablation of the medial half of the left mesencephalon, was sacrificed after 24 days. The inferior colliculus was spared and there was no interruption of the cerebral peduncles. Resulting degeneration of both rubrospinal tracts, tectospinal tracts and the homolateral intersitiospinal tract was observed.

Cat H 2934, ablation of the right vestibular nuclear complex, was sacrificed after 31 days. Resulting degeneration of the vestibulospinal tract and vestibulospinal fibres, in the medial longitudinal fascicle of the right side, was observed.

Operations were carried out under aseptic conditions. For the anesthesia E v i p a n was used and administered intraperitonially in doses amounting to about 1 cc of a ten per cent solution per kilogram bodyweight. This anesthesia proved to be very satisfactory in the majority of the cases. Respiratory death, rather frequent in cats under ether anesthesia, was extremely rare when E v i p a n was used. The longer period of postoperative unconsciousness, typical of E v i p a n in cats, was favorable for the healing of the wound.

In deep anesthesia the thoracic cage of the cats was opened and a cannula inserted in the aorta via the left ventricle. The right atrium was opened and the cats were subsequently perfused with a physiological saline solution to kill them. This saline perfusion was followed by a perfusion with a 10 % formalin solution. This produced a quick hardening and fixation

of the brain and cord, which could subsequently be taken out easily without damage.

METHODS.

In order to get as much information as possible from each of the experiments, the following parts of the central nervous system were prepared. The site of the lesion, in most of the cases, was cut out, embedded in paraffin after dehydration, cut serially at 15 μ and stained with haematoxylin-eosin. Other parts examined were: a slice at the mid-olivary level of the medulla, the transition of the medulla and the cord, comprising the pyramidal decussation down to the second cervical segment, four slices from different levels of the cervical and the thoracic cord, three from the lumbar and one from the sacral cord. Mostly they were prepared for Häggqvist's methylblue-eosin technique because it shows conspicuously the separate fibres, normal as well as degenerated. Bielschowsky's pyridin-silver block impregnation was sometimes used because it took much less time, but after various improvements of Häggqvist's method this advantage became much less. The large block of tissue, containing the pyramidal decussation was cut serially at 6 μ, every tenth section being mounted and stained. Below the level of the hemichordotomy, slices were embedded in paraffin, and Nissl staining with cresyl-violet was carried out to look for chromatolysis. Glees' modification of Bielschowsky's frozen sections — silver impregnation was carried out repeatedly to compare the results with those revealed by the Häggqvist slides. Since Häggqvist's technique was employed as a routine method in this study, a minute description of the modifications practised, will be given.

After the central nervous system had been taken out it was put in 10 % formalin and after a few days the blocks were cut. Initially they were fixed in 30 % formalin, at room temperature for two months, but fixation during 14 days at 37° C. proved to work as well. The same was the case with the subsequent mordation in bichromate which initially was done in 10 % ammonium bichromate for one to two months. This time

could be reduced to one week at 37° C. The entire time, previous to embedding, was reduced to only three weeks, instead of three to four months. Dehydration in alcohol and clearing in xylene, sometimes made the block very brittle, therefore the dehydrating was sometimes done in isopropyl-alcohol. Isopropyl-alcohol can be mixed with water and also it dissolves paraffin, so it can be used to dehydrate as well as to make the block fit for impregnation with paraffin.

Sections were cut serially 6 μ thick, and mounted on glass by means of P. Masson's gelatin—formalin vapour method. Usually the sections stuck to the glass very well with this method, whereas when albumen-glycerin was used, they either came off or showed bubbles and other irregularities which made counting and photographing impracticable.

The mounted sections, were deparaffinized and mordated for one and a half hour at room temperature in a solution, resembling Weigert's rapid mordation (Schnellbeitz), consisting of 90 ml. of a saturated solution of $CrCl_3$ and 210 ml. of 10 % $K_2Cr_2O_7$. After rinsing with distilled water the sections were put in a 20 % solution of phosphomolybdic acid for one hour at room temperature and afterwards rinsed again. Then the sections were put in the staining solution, which consists of a mixture of 45 parts of a 1 % solution of methylblue, 35 parts of a ½ % solution of eosin and 100 parts of distilled water. Formerly the sections were kept in this staining solution from 2 to 7 days at room temperature. One to two hours at 60° C. proved to do as well. After the sections have cooled to room temperature they are put rapidly through 96 % and absolute alcohol and xylene, and without blotting are covered with Canada Balsam. When correctly stained, axons, cells and glia structures will be blue, myelin sheaths and nucleoli brightly red. There is some shrinking of the myelin sheaths, but it can be reduced by fixing in Baker's formalin solution, which contains $CaCl_2$. This technique gives a preparation with considerable contrast in which each nerve fibre is clearly visible. *Even fibres of 1 μ or less in diameter can be easily seen and show their myelin sheath conspicuously.* The thinner the fibre the less brilliantly red the

myelin sheath appears and the myelin sheaths of the finest fibres are stained a dark violet.

Degenerating fibres can easily be distinguished because their axons are either swollen or lacking. When the axons have disappeared the whole fibre area is filled with degenerating myelin material that stains brilliantly red. Eventually this catabolic myelin material also disappears, and *oi areas of old degeneration, blue glia elements are proliferated.* Recent degeneration areas show a red hue at low power magnification because of the absence of axons, while the myelin is still present, and old degeneration is blue because of glial proliferation.

Sometimes *retrograde atrophy* of fibres is marked. Both the myelin sheath and the axon are various in size and have *a flattened appearance. Their cross-sectional area is no longer roundish but eliptic. The myelin sheath, however, keeps its sharp contours and it does not assume the brilliant red hue of the degenerating axon.*

Nissl staining of formalin-fixed and paraffin-embedded material gave good results, if staining was continued for at least thirty minutes in a ½ to 1 % solution of "cresyl-echt-violet", and differentiation in 96 % alcohol was carried out up to 10 minutes if necessary. The slides show a very clear background, with intensily purple Nissl bodies and nucleoli of cells.

The Bielschowsky block-impregnation with silvernitrate was done according to the procedure described in Romeis. All neurofibrils and most of the glia fibres are stained intensely black. Even terminal bulbs are clearly visible. However, it appeared that this technique did not show single degenerated fibres clearly, because the myelin sheath is not visible, a fact which makes the fibres inconspicuous.

Glees' modification of Bielschowsky's technique on frozen sections, shows myelin sheaths to some extend and therefore is preferable. To obtain good results we followed strictly the following points. Before sectioning, the blocks of tissue must be carefully washed to remove the formalin. After sectioning, the sections are washed again and are put in the following mixture for twelve hours at 37° C.: 50 cc of 50 % alcohol + 6 drops

of concentrated ammonia in 50 cc absolute alcohol. After thorough washing in distilled water, impregnation with silver in a 10 % solution of $AgNO_3$ is performed for at least twelve hours at room temperature. This impregnation may be continued for five days, but the optimum is 24 hours. The reduction is effected with 10 % formalin, prepared with tap water. It is important to wash the sections until no more precipitate is formed. Now the sections can be treated with ammoniated silver solution, for ½ to 1 minute. Subsequently the sections should be immediately reduced in 10 % formalin. It is important to prevent the formation of folds in the sections because these cause dark bands. After washing in distilled water, the impregnation is intensified by a solution of three gramms of potassium-rhodanide, and of hypo in 100 cc distilled water. Immediately before use, a few drops of a 1 % goldchloride solution are added. The sections stay in this solution until the gold brown colour changes into a greyish black. After washing the sections are fixed in 5 % hypo. Finally, they are washed three times and carried through alcohol in rising concentration. After mounting the sections are covered with Canada Balsam. Sections treated in this way show nerve fibres very well and make the identification of degeneration relatively easy.

CHAPTER 4.

RESULTS OF THE EXPERIMENTS.

With the knowledge acquired from experiments of many investigators, I tried to find the delineations of the known fibretracts after degeneration, especially in Häggqvist slides. Descending degeneration was brought about by ablation or destruction of the grey centres of origin. In order to study ascending degeneration in the cord, hemichordotomies at successive levels are indispensable.

Massive degeneration in Häggqvist slides shows as a red hue at low power magnification and at high power magnification a degenerated fibre is characterized by either the absence or the swelling of the axon and a marked swelling of the myelin sheath. A degeneration time of at least three weeks is necessary to be sure that all fibres involved show signs of degeneration. In most cases, however, in all fibretracts seemingly normal fibres persist even after degeneration times as long as three months.

Occasionally, single fibres in normal specimens, especially thick ones, look as if they were degenerated when using Häggqvist's technique. For this reason no conclusions can be drawn from isolated degenerated fibres, unless the slide is ideally stained. The above-mentioned facts must be born in mind when analysing degeneration in the central nervous system with Häggqvist's technique.

ASCENDING FIBRESYSTEMS.

The ascending fibres comprise the spinocerebellar, spinothalamic and spinobulbar fibres of different kinds. These groups will be dealt with separately.

The dorsal spinocerebellar tract.

This tract mainly consists of coarse fibres and therefore is easily recognized.

It is generally accepted that the dorsal spinocerebellar tract arises from Clarke's column, situated at the base of the dorsal horn, and that its fibres do not cross. Because Clarke's column does not occur below the third lumbar segment, it has always been assumed that no dorsal spinocerebellar fibres can be found beneath the first lumbar segment. *In the third sacral segment, however, we find a small group of thick fibres in the extremely dorsal tip of the posterolateral funiculus, resembling the dorsal spinocerebellar fibres.* Ascending into the lumbosacral cord, this small group gradually gets larger. Within the sacral cord these fibres are the largest ones present but it is difficult to tell from where they come. Probably they are ipsilateral fibres originating somewhere at the base of the dorsal horn.

In cat H 2572, in which a hemichordotomy was performed at the first sacral segment, these fibres were degenerated rostral to the lesion, and therefore must be ascending fibres (Plate 17, fig. 1). They can be followed cranially where they retain their dorsal position within the dorsolateral funiculus. They soon become intermingled with thick normal fibres, which have their origin cranial to the lesion, without a special localization of the degenerated fibres among the normal ones being noticeable. The degenerated fibres, unexpectedly, become sparser in the higher segments of the lumbar cord. In the lower thoracic segments only a few of them are left, and in the seventh thoracic segment it is doubtful whether any of these fibres are still present. About their termination nothing is known. Possibly they end somewhere in the grey matter. If this is the case they are not spinocerebellar, but propriospinal fibres. *Some of them, however, may proceed farther cranially to a high cervical level.*

In the same cat, at the second lumbar segment, the level of the caudal pole of Clarke's column, many normal thick fibres, originating in this nucleus, course, through and *ventral to the pyramidal tract,* towards the periphery of the cord. In the adjacent higher segments, more fibres join them and these fibres

assemble in a triangular area along the surface of the cord, ventrolateral to the lateral pyramidal tract. Hemichordotomy at the first lumbar segment (cat H 2560, H 2561) is followed by marked degeneration of the fibres in this triangular area (Plate 17, fig. 2). This description applies completely to the dorsal spinocerebellar tract. The thick fibres, at the dorsal tip of the posterolateral funiculus, originating in the lumbosacral cord, caudal to the caudal pole of Clarke's column, are also degenerated. In a low thoracic level the fibres of the dorsal spinocerebellar tract, arising from the caudal extension of Clarke's column, appear to be situated along the surface of the cord in a triangular area, lateral to the rubrospinal tract. *They have fused with the dorsal degenerated fibres and form, together with them, one area of degenerated fibres.* It seems to me that this fasciculus of degenerated fibres has always been taken for the dorsal spinocerebellar tract, though it contains fibres of the segments caudal to Clarke's column.

When following the dorsal spinocerebellar tract upwards into the thoracic cord, no great changes appear to occur in regard to its position. The triangular area, lateral to the rubrospinal tract and the corticospinal tract, increases somewhat in size. A few normal fibres are added to it, but more fibres are added to the dorsal group of fibres. *Normal ones apply themselves to the ventral border of the dorsal part of degenerated fibres* of the dorsal spinocerebellar tract, and furthermore, *considerable intermingling of normal and degenerated fibres occurs.* Fibres of the triangular area shift dorsally and thus the area of connection between the two parts of Flechsig's tract, peripheral to the pyramidal tract, increases in width. In the high thoracic cord these added fibres are rare, but from the second thoracic to the seventh cervical segment, large numbers of normal fibres join both parts of the dorsal spinocerebellar tract. These fibres mainly take their site at the centrally directed border of the tract (Plate 18, fig. 1).

It was impossible at first to indicate a borderline between the dorsal and the ventral spinocerebellar tracts as they fuse to one strand of ascending fibres along the outer surface of the lateral

funiculus. *A chronic lesion* of a fibresystem, however, *appeared to cause a retrograde atrophy of the proximal part of its fibres.* In cat H 2855 the lesion destroyed the complete restiform body but left the brachium conjunctivum intact. The cat survived the operation a long time. The resulting retrograde atrophy of the dorsal spinocerebellar fibres rendered a distinction between them and the unaltered ventral spinocerebellar fibres possible. The border appeared to be situated in the neighbourhood of the border between postero- and anterolateral funiculus (Plate 20, fig. 2 and 3). There was considerable intermingling of both kinds of fibres at the borderline. At the higher cervical segments the degenerated dorsal spinocerebellar fibres lie quite peripherally underneath the pia mater. Unfortunately, they do not indicate the location of the whole dorsal spinocerebellar tract because they are only relatively few. For this reason the ascending degeneration of the dorsal spinocerebellar tract, after a lesion at the eighth cervical segment (cat H 2544, H 2546), will be described.

Just above the lesion the dorsal part of the dorsal spinocerebellar tract appears to be much larger than the triangular part of the tract. The latter is no longer situated at the junction of the lateral pyramidal and the rubrospinal tract, but peripheral to the triangular area of the rubrospinal tract. The reason why many investigators overlooked this part of the dorsal spinocerebellar tract, is because it seems to belong to the rubrospinal tract.

In more cranial segments of the cervical cord, the part of the tract peripheral to the lateral pyramidal tract becomes narrower. At the fourth cervical segment, the area of degenerated fibres, lateral to the rubrospinal tract, has greatly diminished in size and is only represented by a few scattered fibres. Most of the fibres have shifted dorsally and accordingly almost all the fibres lie dorsally in the posterolateral funiculus, where the area occupied by the tract has increased in size. A small number of fibres still lies ventrolateral to the rubrospinal tract. In the cervical cord the apposition of normal fibres to the central border of the dorsal spinocerebellar tract is much less marked

than in the part between the second thoracic segment and the seventh cervical segment. *The normal fibres, which are added to the tract in the cervical cord, freely intermingle with the already present fibres, which are degenerated, with only a slight preference of the former fibres for a central position.*

In the higher segments of the cervical cord intermingling with fibres from the lateral pyramidal tract is obvious. This is clearly demonstrated with a high cervical hemisection of the cord (cats H 542 and H 544) where small bundles of normal pyramidal fibres can be seen lying within a completely degenerated area of dorsal spinocerebellar fibres, rostral to the lesion (Plate 18, fig. 3). The reverse picture can be seen when, following a cortical ablation, the pyramidal tract is degenerated and small bundles of degenerated fibres can be seen surrounded by normal spinocerebellar fibres (cat H 2546, 539, 536).

In the second and first cervical segments the lateral cervical nucleus is present and *degenerated fibres, emerging from the dorsal spinocerebellar tract, can be followed into this nucleus.* At the cranial extension of this nucleus in the lowest part of the medulla, the area occupied by the dorsal spinocerebellar tract has decreased in size. The total number of fibres, present in the dorsol spinocerebellar tract at the third cervical segment, amounts from 10 to 12 thousand. The number of fibres in the tract in a low medullary level lies between 7 and 10 thousand. *Thus two to three thousand fibres contained in the dorsal spinocerebellar tract terminate at that level, presumably in the lateral cervical nucleus where terminal degeneration can be observed* (Plate 19, fig. 1 and 2). A longitudinally cut block of the upper cervical segments, impregnated with silver, clearly showed thick and thin fibres leaving the dorsal spinocerebellar tract, to terminate in the lateral cervical nucleus. These counts and the longitudinal series of the upper part of the cord have been performed by G. G. Schermers, a student working in our laboratory.

Retrograde atrophy of the dorsal spinocerebellar tract, by a lesion of the restiform body, leaves these fibres unaltered, which therefore show conspicuously. (H 2720, 2855; Plate 18, fig. 4).

At the caudal pole of the nucleus of the descending branch

of the trigeminal nerve the dorsal spinocerebellar tract lies ventrolateral to it and is bordered ventrally by the rubrospinal tract. The laterodorsal extension of the lateral reticular nucleus is contained in the tract at this level. It might be possible, although it has not been clearly demonstrated, that some fibres terminate in this nucleus.

The lateral pyramidal tract has disappeared because its fibres shifted medially to form the pyramidal decussation. Over a small area fibres of the dorsal spinocerebellar tract and the rubrospinal tract intermingle.

At the level of the caudal extremity of the olivary nucleus and the beginning of the lemniscal decussation, the degenerated fibres of the dorsal spinocerebellar tract shift dorsally, peripheral to the descending branch of the trigeminal nerve. They are accompanied by fibres from the lateral reticular nucleus of the same side and the inferior olive of the opposite side. In a more rostral level these fibres form the majority of the restiform body in which the fibres of the dorsal spinocerebellar tract keep together and shift dorsally. Some fibres however, lag behind and join the main body of the tract in a much more rostral level. The dorsal spinocerebellar fibres are located dorsomedially in the restiform body.

The ventral spinocerebellar tract.

Generally the name of Gowers is applied to the ventral spinocerebellar tract though he denied its existence.

No special attention has been paid to the question of the origin of the ventral spinocerebellar fibres in this study. Nevertheless, the impression has been gained *that most of the fibres originate from cells in the contralateral ventral horn.*

It is certain that ventral spinocerebellar fibres arise from sacral segments. This is proved by the results of a hemisection of the cord at the first sacral segment (cat H 2572). One can follow rather scattered, degenerated thick fibres from the anterior white commissure around the ventral grey horn to a peripheral position in the dorsal part of the anterolateral funiculus. In a midlumbar level most of these degenerated

fibres have reached this position which they retain throughout the extent of the cord rostrally. These fibres do not lie completely peripherally in the lumbar cord, as they are separated from the pia mater by a strand of thick and thin descending fibres.

After hemisection of the cord at a high lumbar level (cats H 2560 and H 2561) many degenerated fibres, similar in diameter to the spinocerebellar fibres, can be seen in the anterolateral funiculus, mostly at the side of the hemisection. This implies that the fibres have crossed, either in the segment of their origin or one segment higher, as it is generally accepted that the ventral spinocerebellar tract is composed of crossed fibres.

After a hemichordotomy at the first lumbar (cat H 2560) or the twelfth thoracic segment (cat H 2561), ascending degeneration in the anterolateral funiculus, immediately cranial to the lesion, is rather diffusely scattered throughout the complete funiculus. Degenerated fibres are separated from the surface by rather thick normal fibres. Two groups of degenerated fibres can be found. One group lies extremely dorsally in the anterolateral funiculus, encroaching upon the posterolateral funiculus. Its fibres, for the greater part, are rather thick. *Underneath the surface of the cord a bridge-like connection is established with the triangular area of degenerated fibres of the dorsal spinocerebellar tract in the posterolateral funiculus.* It is justifiable to assume that this group of fibres is the first indication of the formation of an area, occupied for the larger part by ventral spinocerebellar fibres. At this level (Th_{12}) however, many normal fibres lie between the degenerated spinocerebellar fibres.

The other concentration of degenerated fibres can be noted in the most ventromedial part of the anterolateral funiculus at about the exit of the ventral roots. In this area many thin fibres are also degenerated. These degenerated fibres are separated from the surface by a conspicuous strand of normal fibres. They will be dealt with in the next sub-chapter.

When following the first group of degenerated fibres cranially in the cord, one sees it concentrating peripherally and dorsally in the anterolateral funiculus. The bulk of fibres lies in the most

dorsal tip of the anterolateral, funiculus in a rather wide area which tapers ventrally into a small fillet of degenerated fibres, mixed with normal ones. This is especially evident in a midthoracic level as can be seen in cat H 2751, and also in cat H 2875 (Plate 20, fig. 1). The most dorsal part is connected with the most ventrally situated fibres of the dorsal spinocerebellar tract by a small peripheral strand of degenerated fibres. Ventrally, the degeneration of the ventral spinocerebellar tract is continuous with an area of degeneration which lies peripherally in the anterolateral funiculus. *At this level a demarcated tract is not yet noticeable since many normal fibres are mixed with the degenerated ones.*

In higher levels, where the ventral spinocerebellar tract becomes more easily visible, it keeps its site in the extreme dorsolateral part of the anterolateral funiculus. Its more or less irregular shape remains approximately the same. Ventrally it tapers into the degenerated area of the anterolateral funiculus proper, dorsally it merges into the degenerated area of the dorsal spinocerebellar tract and medially it gradually merges with the scattered, thin degenerated fibres of the anterolateral funiculus.

So it becomes evident that throughout the extent of the cord the areas of the dorsal and the ventral spinocerebellar tracts touch and fuse. For this reason it is difficult to separate them. At places, however, this is possible because in the area of transition degeneration is more scarce and the fibrepattern shows more thin fibres than in other places. *Moreover, retrograde atrophy of the dorsal spinocerebellar tract makes a more or less sharp demarcation between both tracts noticeable* (Plate 20, (fig. 2 and 3).

In cases of low and midthoracic hemichordotomies a new concentration of degenerated fibres presents itself in a high thoracic level, medial to the peripherally located degeneration. The only possible explanation is that the more peripherally situated fibres are the ones that have already crossed at the level of the lesion, whereas the more centrally lying ones are those that were just crossing at the level of the lesion. If this is the case we have

to assume that the crossed fibres only reach their final position after a course through a number of segments.

At the first thoracic segment the degeneration, in the area of the ventral spinocerebellar fibres, is seemingly less intensive than at lower levels. This is not the case however, for degenerated fibres have not decreased in number, but normal fibres of the same system, arising from levels rostral to the lesion, have reached the area and are found scattered among the degenerated ones. This can be expected to be even more marked at higher segments of the cord. The degeneration is slightly more intense however, in cat H 2749 because the lesion was at a more rostral level and thus interrupted more fibres. At the high thoracic cord it looks as if the complete tract area shifts ventrally. This is caused by the increase in size of the posterolateral funiculus, in the high thoracic and the cervical segments, which is mainly due to the increased number of fibres of its tracts. The anterolateral funiculus, on the contrary, does not show such an increase and therefore occupies a relatively smaller part of the cross-sectional area of the cord in these levels.

At the first thoracic segment the ventral spinocerebellar fibres show some tendency to shift dorsomedially, a tendency which is even more pronounced in low cervical levels. In the sixth cervical segment, therefore, many degenerated ventral spinocerebellar fibres are situated medial to the most ventral fibres of the rubrospinal tract. *They form an area resembling a dorsomedially directed horn-like projection of the ventral spinocerebellar area.* This somewhat unexpected arrangement can best be observed in the animals H 2544 and H 2546 which underwent hemichordotomies at the seventh cervical segment. Since in these cases all the ventral spinocerebellar fibres arising from below this level are interrupted, the delineation of the tract in higher levels can be better studied. In these two cats the horn-like dorsomedial protrusion of the tract presents the same features as in cats H 2560 and H 2561. The degeneration, however, is more pronounced. Because degenerated fibres of the dorsal spinocerebellar tract are present peripheral to the rubrospinal fibes, *normal rubrospinal fibres lie between a peripheral*

and a central strand of degenerated fibres in these segments, belonging to the dorsal and the ventral spinocerebellar tract respectively.

The ventral border of the area of the ventral spinocerebellar tract gradually merges with another area where degeneration it less dense. Medially it is rather difficult to indicate a sharp border-line, for the concentration of degenerated fibres decreases only gradually in a medial direction (Plate 20, fig. 1). In this case, certainly, many fibres belonging to other systems are included in the ventral spinocerebellar tract area. At the fifth and the fourth cervical segment the horn-like protrusion of the tract area recedes again and at the third cervical segment it can no longer be seen.

Nowhere does the dorsal tip of the ventral spinocerebellar tract area pass beyond the horizontal plane through the central canal. The fibres gather against this plane. Dorsally the tract area is wide, tapering ventrally into a rather narrow strand. Such is the aspect of the tract in the highest cervical segments but it is somewhat masked by the uninterrupted strand of degenerated fibres, underneath the pia mater, over the complete lateral funiculus.

From the experiments described it can be concluded that fibres of lower and higher levels intermingle freely, more cranial fibres applying themselves to the medial border of the tract and pushing in between the already present fibres (Plate 20, fig. 1). No other explanation can be offered for the presence of both normal and degenerated fibres of the same diameter everywhere in the ventral spinocerebellar tract area.

Nothing much changes with regard to the position of the tract throughout the transition of the cord and the medulla. In the lower part of the medulla the ventral spinocerebellar tract, traversed by external arcuate fibres, lies peripheral to the lateral reticular nucleus, whereas part of its fibres take their course through it. In a midolivary level, rostral to the lateral reticular nucleus, it looks as if the tract has lost fibres, for its surface area has considerably diminished. *Probably a number of the ventral spinocerebellar fibres have terminated in the nucleus.*

The other ascending fibres and systems of the cord.

No other circumscribed ascending systems can be distinguished in the anterior and lateral funiculus. *Scattered single ascending fibres, however, can be noticed in large numbers.* A few statements concerning their character should be made. Throughout the cord, marked degeneration is found in the peripheral part of the anterolateral funiculus, ventral to the ventral spinocerebellar tract. In the cervical cord this is also the case medial to this tract.

From the experiments described (H 2572, H 2561, H 2560, H 2546, H 2544 and H 2751) it is evident that new fibres are added to this area at all segments of the cord. In the lower levels (sacral, lumbar and lower thoracic) this ascending degeneration is separated from the surface of the cord by normal descending thick fibres between which thin fibres can be seen. At the eighth and seventh thoracic segment, the ascending fibres take their site peripherally, underneath the pia mater. This degeneration area never exceeds one sixth of the width of the anterolateral funiculus. In higher levels it is bordered ventromedially by the normal descending fibres of the direct vestibulospinal tract. In lower levels it extends medially and is bordered medially by the medial longitudinal fascicle. *Nowhere is this area completely degenerated and in all of the experimental cats normal fibres of all sizes can be seen in it.* Possibly, it contains ventral spinocerebellar fibres on their way to the tract area proper, but these are, for the greater part, situated more centrally.

It is maintained that spinothalamic and spinotectal fibres are present in this area. *In a medullary level, however, the only degeneration present, besides the spinocerebellar systems, consists of a few tiny scattered fibres lying between the medial lemniscus and the ventral spinocerebellar tract* (Plate 21, fig. 3). Because the ventral spinocerebellar tract area is smaller at this level than at the first cervical segment, it is highly improbable that the ascending anterolateral fibres run in this tract (Plate 21, fig. 4). Moreover, at a level *rostral to the point where the*

ventral spinocerebellar fibres shift dorsally to join the superior cerebellar peduncle, *no trace of any degenerated fibre can be observed in my experiments.*

All the ascending fibres present in the anterolateral funiculus, outside the ventral spinocerebellar tract, terminate in the lower part of the medulla. These fibres become dispersed when the lateral reticular nucleus is formed, and many degenerated fibres can be observed around the cells of this nucleus (Plate 21, fig. 2).

Because the cells of the lateral reticular nucleus degenerate and disappear after a chronic cerebellar ablation, we must assume that all efferent fibres from the nucleus project on the cerebellum. *The lateral reticular nucleus must be, therefore, mainly a relay in the ascending anterolateral fascicle of Gowers.* Other fibres of the fascicle, namely the thinner ones, can be seen terminating in the neighbourhood of small reticular formation cells, surrounding the lateral reticular nucleus in its level and rostral to it (Plate 21, fig. 3). *It seems probable that these cells are those which send their axons to the tectum and thalamus. In this way an interrupted pathway from the spinal cord to the tectum and thalamus must be present in the cat since direct connections could not be found.*

In the anterior funiculus there are ascending fibres which degenerate after a lumbar hemisection of the cord. They are not very numerous and mainly of small size, not surpassing 5 μ in diameter. In the thoracic cord they are situated underneath the pia mater along the anterior medial fissure where they separate the medial longitudinal fascicle from the surface. At the transition of the thoracic and the cervical cord these fibres shift laterally, along the surface of the cord and assume a peripheral position in the ventral aspect of the anterior funiculus (Plate 25, fig. 3). At the first cervical segment the number of these fibres suddenly increases greatly. These additional fibres have been observed in a state of degeneration in cat H 542 where a hemichordotomy was performed at the second cervical segment (Plate 18, fig. 5). Degeneration in the anterior funiculus was contralateral to the lesion and was due to the destruc-

tion of the caudal part of the lateral cervical nucleus. In normal specimens the efferent fibres from the lateral cervical nucleus have been observed to cross in the anterior white commissure and, after crossing, to proceed underneath the pia mater in the anterior medial fissure to their position in the ventral part of the anterior funiculus (Plate 19, fig. 3). *These fibres, together with the above-mentioned fibres from lumbar levels in the anterior funiculus, can be followed to the caudal part of the inferior olive, where they terminate.* They enter the inferior olivary complex from its ventral side (Plate 18, fig. 5), and are gradually replaced by the most lateral fibres of the medial lemniscus. A spino-olivary connection has thus been demonstrated though it is rather scanty. The connection of the lateral cervical nucleus with the contralateral inferior olive, however, appears to be massive. This latter connection will be called the c e r v i c o - o l i v a r y s y s t e m, and the afferent fibres to this nucleus, contained in the dorsal spinocerebellar tract, the s p i n o c e r v i c a l s y s t e m.

Closely rostral to a transverse section at any level of the cord, a number of degenerated fibres can be observed in a part of the white matter, not occupied by circumscribed tracts. Although degenerated fibres are rather numerous normal fibres surpass them everywhere in quantity. Immediately around the grey matter this degeneration already disappears within one segment (Plate 27, fig. 2). Two or three segments above the lesion, more peripherally situated degenerated fibres also have disappeared. This degeneration must be attributed to ascending propriospinal fibres. *In general, the most peripheral of these propriospinal fibres are the longer ones as well as the thicker ones.* Many propriospinal fibres surpassing more than three segments in length possibly take a course together with the already described ascending fibresystems but if so, they can not be distinguished from them either by their diameter or by their degeneration after hemichordotomies.

DESCENDING TRACTS AND FIBRESYSTEMS.

The descending tracts and fibresystems of the cord, originating outside it, are: the pyramidal tract, the rubrospinal tract,

the medial longitudinal fascicle, the vestibulospinal tract and a number of reticulospinal tracts or systems. The origin of the majority of these tracts is generally known and needs no further specification in the scope of this thesis. Some specifications will be given, however, on the medial longitudinal fascicle and the reticulospinal connections.

The pyramidal tract.

The pyramidal tract has been studied for many decades and most of its features have been the subject of investigation. In this thesis only its fibre composition and its topical relationship to the surrounding fibresystems, with the interchange of fibres in the cord, will be commented upon.

In cases of severance of the tract rostral to the medulla, the degenerated medullary pyramid is situated ventrally, in the usual way, as a circumscribed bundle at the side homolateral to the lesion. No important intermingling can be found with neighbouring systems such as the medial lemniscus. When we look at the level where the pyramidal decussation begins, the first fibres forming the medial lemniscus are present. These medial lemniscus fibres also cross and after their crossing are found at the lateral side (peripherally) of both crossing pyramidal tracts. The pyramidal tract crosses in bundles, alternating with those of the contralateral one. The crossing measures about one centimeter from its rostral beginning to its caudal end. In a level somewhat caudal to the rostral beginning the crossing degenerated pyramidal bundles are accompanied by normal fibres, belonging to the system connecting the lateral cervical nucleus with the contralateral inferior olive. The latter fibres assemble in an area, lateral to the still uncrossed pyramidal fibres and should not be mistaken for medial lemniscal fibres (Plate 19, fig. 3).

The pyramidal bundles, after having crossed the midline, traverse the grey matter, in a dorsolateral direction, to reach the posterolateral funiculus of the cord. Rostral to the level of the pyramidal crossing, the dorsal spinocerebellar and the rubrospinal tract lie side by side in this funiculus, the latter ventral

to the fomer. A number of crossed pyramidal bundles penetrates between both tracts when entering the posterolateral funiculus and separate the one from the other. Most of the rubrospinal fibres are pushed ventrally by the pyramidal fibres. A small number of them comes to lie at the borderline of the lateral pyramidal and the dorsal spinocerebellar tracts, for the greater part among the fibres of the former one (Plate 23, fig. 1). A few of the pyramidal bundles proceed to the periphery of the cord, where they mix to some degree with the fibres of the dorsal spinocerebellar tract and otherwise divide this tract in two parts. The phenomena described lead to intermingling of pyramidal, dorsal spinocerebellar and rubrospinal fibres in the lateral third of the posterolateral funiculus of the cord.

At the third cervical segment, however, the most laterally located bundles of the lateral pyramidal tract recede medially and join the main part of the tract, in the centre of the posterolateral funiculus. The lateral pyramidal tract at C_4, therefore, is united again to one fibretract which is bordered dorsally and laterally by the dorsal spinocerebellar tract and ventrally, partly by the rubrospinal tract and partly by ill-defined, probably reticulo- and propriospinal, fibres. Medially the lateral pyramidal tract is separated from the posterior horn by a strand of thin fibres which normally can only be distinguished with difficulty from the pyramidal fibres. In all probability these are relatively short propriospinal fibres, since it is difficult to cause them to degenerate, even with high chordotomies.

With regard to its fibre content the pyramidal area is rather homogeneous at a high cervical level, with the exception of its lateral third where small numbers of rubrospinal fibres are found. At its borders the usual interchange of fibres with adjacent areas, however, is clearly visible. In one cat (H 2748) a glial membrane separated the lateral pyramidal from the dorsal spinocerebellar tract, interchange of fibres between both tracts, therefore, in this specimen was prevented.

An uncrossed anterior pyramidal tract, as a rule, does not exist in the cat. In the specimens (except cat H 2671) in which one pyramid was degenerated, no trace of degeneration within the

anterior funiculus was present. In cat H 2671 however, a small anterior pyramidal tract could be traced down to the middle of the cervical cord. In lower levels it was no longer found. Moreover, it was only present at one side and therefore can be regarded as an abnormality.

Usually all of the pyramidal fibres cross in the cat with only a small number of fibres proceeding to the ipsilateral posterolateral funiculus (Plate 22, fig. 1). The grey matter between the posterior and the anterior horn at the level of the pyramidal decussation is very reticular in structure. Many thin fibres, united in small scattered bundles, are found between the cellular elements. Many pyramidal fibres are directed to this reticular formation, mainly to the part nearest to the posterior horn. These fibres can be traced easily when degenerated (Plate 22, fig. 2). Within a very small distance they are lost in this reticular formation and probably many pyramidal fibres terminate in this region. Some other pyramidal fibres are directed immediately to the lateral border of the anterior horn, where they soon are lost also. The proof of the termination of a number of pyramidal fibres is to be seen in the decrease of the total number of fibres, contained in the tract. In a low medullary level there are 40 to 80 thousand fibres in the tract, of which at the third cervical segment only 30 to 50 thousand fibres are preserved. As will be seen below, new fibres join the pyramidal tract, both at and below the decussation, and therefore it is evident that many more fibres of pyramidal nature terminate at the level of the decussation.

At the third thoracic segment the lateral pyramidal tract still lies in the centre of the posterolateral funiculus, but its fibres have decreased to about half its number in the first cervical segment. The fibres, no longer present, presumably proceeded to the cervical intumescence. The tract is bordered laterally and lateroventrally by the dorsal spinocerebellar tract. In its lateral and lateroventral parts thick rubrospinal fibres, which exceed the pyramidal fibres in diameter, are very conspicuous.

During its descent from the third thoracic segment to the

lumbar cord the number of fibres within the lateral pyramidal tract area does not decrease very much. At the tenth thoracic segment the dorsal spinocerebellar tract divides into a dorsal and a ventrolateral part and pyramidal fibres again come to lie along the periphery of the posterolateral funiculus. Besides this, the rubrospinal tract, as such, does no longer exist and *the majority of the remaining rubrospinal fibres are found within the lateral half of the pyramidal tract area* (Plate 24, fig. 1). A small number of rubrospinal fibres lie just ventral to the lateral pyramidal tract, medial to the ventral part of the dorsal spinocerebellar tract. The area of the lateral pyramidal tract at this level is elliptical in shape, the long axis directed mediolaterally. Its medial half is composed of pyramidal and propriospinal fibres. Within its lateral half numbers of thick rubrospinal fibres are found.

In the upper part of the lumbar intumescence, comprising the third and fourth lumbar segments, the majority of the pyramidal fibres leave the tract area and below the fifth lumbar segment there are no degenerated pyramidal fibres to be found in it (Plate 22, fig. 5).

In cases of hemichordotomy, even when performed at a high cervical level, however, *degeneration in the centre of the posterolateral funiculus*, apparently similar to that following intracranial pyramidal tract severance, *can be followed much farther downwards* (Plate 22, fig. 4). This is more marked the lower the level of the chordotomy. Differences in degree and extent of fibre degeneration, within the pyramidal tract area, after severance at different levels, will be described in order to determine the fibre content at the levels under consideration.

The above description was a summary of the results of the experiments on cats H 536, H 2546, H 2849, H 2892, H 2536.

After ablation of only the motor cortex (cats H 2546 and H 2949) many thin fibres are preserved within the medullary pyramid, even after very long degeneration times. This is much more so in the area of the lateral pyramidal tract in the cord, where about half of the fibres are preserved. Total decortication is followed by a much more severe degeneration in the medullary

pyramid and only small numbers of very thin fibres are left intact (cat H 2892 f. e.). In this case also more fibres, not restricted to very thin ones, are preserved in the area of the lateral pyramidal tract. These experiments demonstrate the long known fact that most of the pyramidal fibres arise from the motor cortex, but that an appreciable number of them arises from other parts of the cerebral cortex. With total ablation of a cerebral hemisphere or severance of a cerebral peduncle the number of degenerated fibres, in the medullary pyramid as well as in the lateral pyramidal tract, does not increase appreciably when compared to that after complete cortical ablation. *Therefore, it is highly improbable that fibres of the pyramidal tract arise from some nucleus between the cortex and the mesencephalon.*

We already saw that many fibres are added to the pyramidal tract during the decussation. These added fibres degenerate only after a hemisection at the first cervical segment but do not degenerate when the pyramidal tract is severed in a level rostral to the pyramidal decussation. This explains the heavier degeneration in the lateral pyramidal tract area after a hemichordotomy than after a cortical ablation. This difference is noticeable even in low cord levels (Plate 22, fig. 5 and 6). These foreign fibres, however, can not replace completely the number of pyramidal fibres, terminating at the level where the former fibres arise. The additional fibres amount to about 20 to 30 % of the fibre population of the pyramidal area in the cervical cord and chiefly are of thin and small medium-sized calibres.

Although a high chordotomy causes an almost total fibre degeneration of the area of the lateral pyramidal tract in the adjacent caudal segments, normal fibres of small sizes can be found in it a few segments below the lesion. These fibres gradually increase in number and at a midthoracic level there are many of them. Since in the lumbar segments the majority of the rubrospinal fibres comes to lie also in the pyramidal tract area, its fibre content at that level is rather heterogeneous. The size of the pyramidal tract area gradually diminishes, its shape

being round in the cervical cord and flattened in a dorsoventral direction in the lumbar cord. The fact that the size of its cross-surface area remains unchanged during its descent in the thoracic cord, presumably, may be attributed to the number of terminating pyramidal fibres and those of the foreign fibres, joining it, being about equal.

The fact that *the pyramidal tract area degenerates farther downwards following a chordotomy than after severance at a supraspinal level* can not be explained by pyramidal fibres being cut in larger numbers in the cord. This can especially not be so as a low chordotomy is followed by a degeneration of greater length than a high one. In cases of lumbar chordotomy degeneration of thin fibres in the pyramidal tract area can be traced down into the coccygeal segments (Plate 22, fig. 4). The fibres degenerating so far downward certainly are the ones joining the lateral pyramidal tract area at low levels. Whether or not they are functionally related to it is as yet unknown. A second neuron is in principal acceptable since many of the pyramidal fibres do terminate on some intercalated nerve cells in the cord. Especially in animals in which the pyramidal tract ends in the upper cervical cord, second neuron fibres descending in to the cord do not seem incomprehensible.

The rubrospinal tract.

The tract originates completely or chiefly from large neurons within the caudal part of the red nucleus, which, in all probability, chiefly contributes thick fibres to the tract. Immeditely after originating from the cells these fibres cross to the opposite tegmentum where they form a very loosely arranged group of thick fibres, intermingled with moderate numbers of much thinner ones. These thinner fibres, for the greater part, degenerate after destruction of the greater part of the ipsilateral mesencephalon. In lower levels, however, many thin fibres are again found between the thick ones (cat H 2760). *Therefore, the thin fibres, present within the area of the rubrospinal tract, mostly do not belong to the rubrospinal system.* In cat H 2933 they are degenerated, because the lesion destroyed most of the mesence-

phalic tegmentum. Even in a low level many more fibres than the rubrospinal ones are degenerated (Plate 24, fig. 3).

In both cats most of the thick rubrospinal fibres were degenerated, contralateral to the lesion, and could be easily distinguished from the normal thin fibres of the tract. In the medulla the rubrospinal tract is situated laterodorsally to the ventral spinocerebellar tract. A considerable intermingling occurs between both systems where they meet. The surface occupied by the rubrospinal tract now has the shape of a triangle with its base directed laterally towards the external arcuate fibres, and its apex medially. The thick degenerated fibres are wide apart, separated from each other by, presumably, reticular fibres.

A nucleus develops in the tract area and this causes an even greater separation between the different fibres. This nucleus is a lateral and rostral continuation of the large lateral reticular nucleus. From experimental cats the impression has been gained that the thin fibres of the tract probably terminate in this part of the nucleus.

Caudal to this nucleus the tract surface area gets much larger when compared to its original surface. This is due to large numbers of normal fibres, which probably arise from the lateral reticular nucleus or its surroundings, joining it. Thus the thick fibres alone, numerically a minority, belong to the rubrospinal tract proper. The added fibres descend into the spinal cord together with the rubrospinal fibres (Plates 23, fig. 2).

In low medullary levels the dorsal spinocerebellar tract came to lie closely dorsal to the rubrospinal tract. Fibres of both tracts intermingle at the border-line. Between the outer surface of the medulla and the rubrospinal tract the external arcuate fibres run, with small numbers of both spinocerebellar and rubrospinal fibres enclosed between them.

The rubrospinal tract area retains its position and triangular shape during the transition of the medulla into the spinal cord. At this transition the crossing bundles of the pyramidal tract penetrate between the rubrospinal and the dorsal spinocerebellar tract and separate them. Intermingling of the fibres of the latter tracts, therefore, comes to an end but, subsequently, rubrospinal

and pyramidal fibres can be seen to mix. The majority of the rubrospinal tract fibres are pushed ventrally, their area however, retains its triangular shape. A few fibres escape this ventral shift and can be found in the laterodorsal part of the lateral pyramidal tract (Plate 23, fig. 1). In normal specimens these rubrospinal fibres can not be recognized because they are about equal in size to those of the dorsal spinocerebellar tract. Initially therefore, intermingling of pyramidal and dorsal spinocerebellar fibres at the laterodorsal border of the lateral pyramidal tract was suspected. Degeneration experiments of the rubrospinal tract however, proved these thick fibres to be rubrospinal.

The ventral tip of the rubrospinal tract shows a ventral extension because the fibres remain blended with those of the ventral spinocerebellar tract. Between the lateral margin of the rubrospinal tract and the outer surface of the cord a small strand of ascending fibres is found, connecting the ventral and the dorsal spinocerebellar tracts. This strand of fibres has already been described in the previous chapter. *From the description it is clear that the rubrospinal fibres have a rather large dispersion area dorsoventrally*, since the most dorsal ones touch the posterior horn and the most ventral ones encroach upon the anterolateral funiculus. The location of the degenerated rubrospinal fibres, as described, was found in cat H 2760 and H 2933. Presently, the features of the rubrospinal tract in the lower segments of the cord will be discussed with the help of the slides obtained from these cats, completed with those from cats H 2804 and H 2814.

In the lower segments of the cervical cord the following changes are present in the area occupied by the rubrospinal fibres. From the medial tip of the area thick fibres penetrate into the pyramidal tract area and almost everywhere in the pyramidal area thick degenerated rubrospinal fibres can be found, though most of them are situated in its lateral part. Lateral to the rubrospinal tract spinocerebellar fibres accumulate, and in the lower part of the cervical cord a more or less triangular area of spinocerebellar fibres protrudes medially into

the tact area. Rubrospinal fibres continue to enter the pyramidal tract over the entire extent of its course through the cord.

In the first thoracic segment rubrospinal fibres shift dorsally in such a way that the anterolateral funiculus becomes free of them. In the next thoracic segments, however, fibres reenter it, mixed with ventral spinocerebellar fibres. Occasionally a few rubrospinal fibres can be found in the area of spinocerebellar fibres, lateral to the rubrospinal tract.

In the lower part of the thoracic cord the rubrospinal fibres, greatly diminished in number, are found ventral and medial to the large accumulation of dorsal spinocerebellar tract fibres and in the lateral part of the pyramidal tract area. Only about half of the rubrospinal fibres proved to lie outside the pyramidal tract area. *In the uppermost lumbar segments the majority of the rubrospinal fibres can be seen within the lateral part of the pyramidal tract area* (Plate 24, fig. 1). Only some fibres lie ventral to it, mixed with the lowermost spinocerebellar tract fibres arising from the caudal extremities of Clarke's column. In the lower lumbar segments the rubrospinal fibres are located along the periphery of the cord ventrolateral to the area of thick ascending fibres. A small number of them can be followed into the sacral segments, thus extending farther caudally than the pyramidal fibres.

The medial longitudinal and the predorsal fascicle.

The medial longitudinal fascicle is very large and highly developed in the medulla and the cervical cord of the cat. Its composition can not be explained without studying its course through the brain stem and taking into account the contribution of the fibres from the predorsal fascicle.

The most rostral contingent of the medial longitudinal fascicle was found at a very rostral oculomotor nuclei level of the mesencephalon. It consisted of a number of thick fibres arising from the ipsilateral interstitial nucleus of Cajal. After destroying this nucleus (cats H 2760 and H 2933) these fibres were totally

degeneration ipsilateral to the lesion, a fact which proves them to be uncrossed. At a mid oculomotor nuclei level many fibres of smaller sizes joined the thick ones. These fibres were mainly ascending ones, since severing them did not increase degeneration in high pontine levels (cat H 2933).

The predorsal fascicle was found only caudal to the oculomotor nuclei. It consisted of reticular formation bundles, near the raphe, which contained the thick tectospinal fibres arising from the contralateral superior colliculus (cat H 2505, H 2729 and H 2760). So far as could be established, fibres from the inferior colliculus did not join either the medial longitudinal fascicle or the predorsal fascicle. In the pontine tegmentum both fascicles fused, the tectospinal fibres finding their site at the ventral aspect of the medial longitudinal fascicle. New stray fibres joined the fascicle or left it, but major changes in its fibre content did not occur.

At the high medullary level of the vestibular nuclei large numbers of fibres were contributed to the fascicle. Unfortunately, no lesions of the separate vestibular nuclei were carried out. In each of the cats H 2570, H 2855 and H 2934 different parts of the vestibular nuclear complex were damaged but never was there the involvement of one circumscribed nucleus. Comparisons between these cats and close observation of the normal slides of the medulla, however, made it possible to obtain an impression of the localization of the vestibular fibres from the different parts of the nuclear complex. In most cases the medial and lateral vestibular nuclei were destroyed, together with either a large part of the descending nucleus or of the ascending nucleus.

Comparisons indicated that the fibres from the medial and descending nuclei were equally distributed over both the ipsilateral and the contralateral medial longitudinal fascicle. Most of the fibres from the medial nucleus were crossed and the greater part of those from the descending nucleus were uncrossed. Initially, the crossed fibres from the medial nucleus lay in the mediocentral part of the fascicle and the uncrossed fibres, from the descending nucleus, lay, for the greater part,

completely dorsal in the fascicle. They pushed the interstitiospinal fibres ventrally. At higher levels the latter fibres lay dorsal in the medial longitudinal fascicle.

The lateral vestibular nucleus contributes a small number of chiefly uncrossed fibres to the medial longitudinal fascicle, but they are not confined to a definite part of it. The ascending vestibular nucleus sends some descending fibres in the fascicle but they soon have the fascicle again and, therefore, are of no importance in this study.

The enormous amount of vestibulospinal fibres, together with large numbers of reticulospinal fibres, joining the medial longitudinal fascicle, make it the largest tract in the lower half of the medulla. The localization of fibres of different origin is indistinct because fibres from different sources intermingle to such an extent that *intermingling seems to be the chief characteristic of the fibre composition of the medial longitudinal fascicle.* When attempting to locate the fibres of different sources it shrould be kept in mind that one will be lead to a schematization of the real structure.

The experiments on cats H 2505, H 2591 and H 2729 show that the tectospinal fibres are scattered over the lateral part of the ventral half of the medial longitudinal fascicle. The interstitiospinal fibres, degenerated in cats H 2760 and H 2933, are situated medially in the ventral part of the dorsal half of the fascicle. These two kinds of fibres are not grouped together in distinct small bundles but lie solitarily between other fibres of about equal sizes, even though the majority of them are found in a special part of the fascicle. The fibres of the descending vestibular nucleus lie entirely dorsal in the fascicle, whereas the fibres of the medial vestibular nucleus lie both ventral to the interstitiospinal fibres and very medially. At the lateral margin of the fascicle new fibres enter it, over the entire length of the medulla, from the reticular formation just lateral to it. This lateral side is, therefore, only vaguely circumscribed and irregularly shaped. The fibres, presumably originating in the medullary reticular formation, enter the tract assembled in small groups or bundles. In more caudal levels they gradually become dis-

persed among the fibres already present in the fascicle. These reticulospinal fibres are degenerated in cats H 2843, H 2671 and a few others, in which they could be followed, within the fascicle, into the cervical cord. *The addition of reticular fibres to the fascicle is followed by a change of the fibrepattern.* In a high level almost all its fibres are very thick but at a lower level, when the reticulospinal fibres have joined it, many thin fibres are present between the thick ones (Plate 25, fig. 1 and 2).

At a caudal olivary level the medial longitudinal fascicle is a large tract, and is lying closely to the raphe, elongated in a dorsoventral direction. Dorsally it touches the floor of the 4th ventricle at its transition into the spinal central canal. Its lateral margin is irregular in shape and gradually merges into the reticular formation. Ventrally, the fascicle is bordered by the medial lemniscus. There is a general tendency of the fibres of the medial longitudinal fascicle to shift ventrally, probably because most of the fibres enter the fascicle dorsally and push the already present fibres ventrally. In the lower part of the medulla a lateral shift of the ventral part of the fascicle can be observed, and the topography of the tract is completely changed. The disappearance of structures lying ventrally in the medulla, such as the pyramidal tract, the medial lemniscus and the inferior olives, and the appearance of the nuclei of the dorsal funiculus, explain the ventral position of the medial longitudinal fascicle in the lower medulla and the spinal cord.

In the cervical cord the fascicle occupies most of the medial and ventral part of the anterior funiculus. It is separated from the surface of the medial anterior fissure by a strand of fibres originating from the contralateral lateral cervical nucleus. It extends so far laterally that it almost encroaches upon the anterolateral funiculus and, therefore, part of its fibres lie dorsal to the direct vestibulospinal tract. The most dorsally situated fibres of the medial longitudinal fascicle terminate at the transition of the medulla into the cord. Other fibres lying dorsally shift ventrally: a general tendency of the fascicular fibres. In this way the interstitiospinal fibres come to lie dorsally again in the medial longitudinal fascicle (Plate 25, fig. 5). These

interstitiospinal fibres, however, are separated from the anterior white commissure by propriospinal fibres, not belonging to the medial longitudinal fascicle.

In the caudal part of the cervical cord the medial longitudinal fascicle has fused with the vestibulospinal tract and a border-line between the two tracts is no longer visible. The most dorsal part of the fascicle contains some interstitiospinal and many propriospinal fibres. The existence of the latter fibres is derived from the fact that they are not degenerated in the above-mentioned animals. Only a chordotomy is able to cause them to degenerate. They, therefore, should be considered as descending fibres originating in the lower medulla, presumably from reticular formation neurons.

More than half of the fibres of the medial longitudinal fascicle terminate in the cervical cord, at least they leave the fascicle there. Many of the remaining ones do the same in the rostral thoracic segments. Interstitiospinal fibres can be followed, in the dorsal part of the fascicle, as far caudally as the 7th cervical segment. The tectospinal fibres can be followed caudally, scattered in the ventral and lateral part of the fascicle, as far as the second thoracic segment (Plate 25, fig. 4). The reticulospinal fibres contained in the medial longitudinal fascicle also terminate in the cervical cord. Therefore, the medial longitudinal fascicle, in the thoracic cord contains only vestibulospinal fibres.

The medial longitudinal fascicle in the cord always seems to be larger in normal cases than in cases where its size is indicated by degenerated fibres, presumably because it is surrounded by an area in which fibres occur similar in size to the large ones of the fascicle. Such were those, already mentioned, lying dorsal to it and they proved to be especially numerous in lumbar segments.

In the sacral segments degenerated fibres from the vestibular nuclei are scattered between large numbers of fibres, similar in size, originating from spinal levels. These scattered fibres represent what is left of the medullary medial longitudinal fascicle. What looks like the medial longitudinal fascicle at this level has almost no fibres in common with the fascicle in a

medullary level. More fibres are degenerated in the fascicle after chordotomies, and at sacral levels the degeneration is heavier when the level of the chordotomy is situated in more caudal segments. The change in fibre content is already considerable in the thoracic cord, where moderate numbers of vestibulospinal fibres and some tectospinal ones are the only fibres of supraspinal origin. The lateral shift of fascicular fibres and the addition of propriospinal fibres of similar diameters are the cause of the fact that the border between the vestibulospinal tract and the medial longitudinal fascicle can no longer be seen, from the cervical cord downwards. The vestibulospinal fibres contained in the medial longitudinal fascicle are the longest descending fibres, present in the spinal cord, for they are still present in coccygeal segments.

The description shows conclusively that *the medial longitudinal fascicle is a heterogeneous tract over whole its length, in which fibres of different origin travel.* These are mostly descending fibres, originating and terminating at all levels of the brain stem and the cord. Most of them are thick fibres but nowhere are thin fibres entirely absent. The origin of the thinner fibres could not be established because they are less conspicuous and can not be readily followed from their origin into the fascicle. Over the entire length of the cord bundles of thin ascending fibres are present between the surface of the cord and the medial longitudinal fascicle. These are ascending propriospinal and spino-olivary fibres. In the scope of this thesis only the medullary and spinal part of the medial longitudinal fascicle have to be considered.

The vestibulospinal tract of Deiters.

The vestibulospinal tract arises chiefly from the large neurons of the ipsilateral lateral vestibular nucleus of Deiters. Similar to the rubrospinal fibres they do not unite to one compact bundle but shift to their position separately, in small groups, accompanied by numbers of fibres of various sizes. The fibres assemble, more or less, just lateral to the inferior olive, but still are scattered over an area, also containing large amounts of

reticular formation elements. In a low olivary level the tract becomes more compact, because the reticular elements, lying between its fibres, grow less numerous. The most ventral fibres of the tract mix with the most lateral ones of the medial lemniscus and more caudally with the cervico-olivary fibres, which take the place of the medial lemniscal fibres. This is demonstrated by the experiments in cats H 2570, H 2855 and H 2934, from which it also appears that *only the thick fibres belong to the direct vestibulospinal tract.* These thick fibres are found within small bundles, containing large numbers of fibres of smaller sizes which presumably belong to the reticular formation, through which the vestibulospinal fibres travel. These thinner fibres accompany the thick fibres of the tract into the cord, where they rapidly diminish in number.

In the upper cervical cord the vestibulospinal tract is found in the most lateral part of the anterior funiculus, along with a lateral extension, encroaching upon the lateral funiculus (Plate 26, fig. 1). Ventrally the tract touches the ventral surface of the cord only in its medial part, whereas the lateral part of the tract deviates dorsally as a hornshaped process. At that place thin ascending fibres lie peripheral to the descending vestibulospinal fibres. Dorsally, the tract gradually merges into the surrounding white matter and the medial border of the tract appears to lie just medial to the exit of the ventral roots.

In the cervical cord, down to the 7th cervical segment, the number of fibres diminishes considerably and caudal to this segment only about ¼ of them are left. The vestibulospinal fibres appear to be located along the periphery of the ventral margin of the cord, and anterior root fibres traverse them (Plate 26, fig. 2).

In the upper thoracic cord the fibres shift dorsolaterally along the periphery, penetrating deeply into the anterolateral funiculus as almost to reach the posterolateral funiculus. They receed again ventromedially in lower levels. In the experimental animals mentioned, the degenerated fibres were found to lie underneath the pia mater, separately, without assembling into small groups or bundles, from the 7th cervical segment on down-

wards. Many normal fibres were found between the vestibulospinal fibres and a tract in the classical sense, therefore, could no longer be distinguished at that level. This was all the more so as a sharp border-line between the vestibulispinal fibres and the medial longitudinal fascicle could not be distinguished.

In the lumbar cord vestibulospinal fibres are confined to the medial aspect of the tract area, as seen in the cervical cord, and it is hard to tell whether they belong to the medial longitudinal fascicle or to the direct vestibulospinal tract. Fibres leave the tract at all levels of the cord, bending dorsally through the anterior funiculus to terminate around cells in the anterior horn. The direct vestibulospinal fibres probably do not descend below the lumbosacral intumescence.

The other descending fibres of the cord.

In the chapter about the ascending fibres it has already been emphasized that many fibres do not belong to the well-known tracts or pathways. With regard to the descending fibres the same statement has to be made as a large number of fibres prove to lie outside the tracts and pathways described.

In 1926 Papez described three different reticulospinal tracts, originating in the reticular formation of the mesencephalon, the pons and the medulla. The study of the cats H 2637, H 2659, H 2671 and H 2843, in which lesions of the brain stem reticular formation have been brought about, confirmed his statement only partly. Reticulospinal fibres prove to be rather numerous in the areas he indicated, but neither were they absent outside of these areas nor did they constitute the majority of the fibres within them. *The reticulospinal fibres are not united in more or less compact tracts.* None of the small bundles, occurring in the areas attributed to them, consists chiefly of them. In the cord a certain degree of concentration of reticulospinal fibres is found ventral to the rubrospinal tract, between the medial longitudinal fascicle and the vestibulospinal tract (H 2843), and within the medial longitudinal fascicle itself. These locations correspond to some extent with the tracts

indicated by Papez but otherwise *such fibres were found everywhere in the anterior and the anterolateral funiculus.* (Plate 24, fig. 4).

Except for the fasciculus proprius, nearly one half of the white matter of the anterior and anterolateral funiculus, not occupied by circumscribed tracts, contains reticulospinal fibres descending from the lower part of the medulla into the cord. These fibres, however, can not be followed beyond the second cervical segment. The fibres within the three areas of Papez, in which I found a larger concentration of reticulospinal fibres, could be traced farther downwards, but they also terminated soon afterwards. The reticulospinal fibres between the medial longitudinal fascicle and the vestibulospinal tract appeared to descend farthest into the cervical intumescence.

Furthermore, many reticulospinal fibres are contained within the rubrospinal and the direct vestibulospinal tract and it seems probable that these fibres are the longest reticulospinal fibres, present in the spinal cord, although no direct evidence has been presented on this subject. The phenomenon that the degeneration in the well-known tracts, descending into the cord, is more abundant after severance of them in a low medullary level than after destruction of their origin, is a point in favour of this opinion. Gradually these reticulospinal fibres become replaced by propriospinal fibres. The presence of reticulospinal fibres in the medial longitudinal fascicle could be established by the change in fibre composition caudal to the level where thin and medium sized fibrebundles, that in a low medullary level lay beside the fascicle, penetrated into it and intermingled with the other fibres of the fascicle.

A category of fibres deserving some attention are those of the so-called fasciculus proprius of the cord surrounding the anterior horn. About one segment caudal or cranial to a chordotomy this fascicle is especially distinct because it is the only area which is nearly free from degenerated fibres (Plate 27, fig. 2). It could be concluded, therefore, to consist of very short propriospinal fibres. Study of slides very near a chordotomy show it to consist of both ascending and descending fibres in

equal numbers. More details about the fasciculus proprius will be given when the results of double ipsilateral hemichordotomies are reported.

The anterior funiculus does not contain outstanding long descending propriospinal systems apart from those located just dorsally to the medial longitudinal fascicle (Plate 27, fig. 1). Within the area of this fascicle, however, gradually descending propriospinal fibres replace those arising from the brain stem such as the vestibulo-, tecto-, and interstitiospinal ones.

In cases of high cervical chordotomy the anterolateral funiculus exhibits scattered degenerated fibres of all diameters. From these observations, and the ones reported in the preceding chapters, it can be concluded that it consists chiefly of solitary ascending and descending fibres, not united into bundles or tracts, its fibre population changing at every level. Between these fibres those of the long ascending and descending systems pass through it on their way between the areas and the central grey matter. These fibres, belonging to known systems, are especially numerous in the low thoracic cord and belong mainly to the tract of Gowers (Plate 27, fig. 1). They are responsable for the fact that the number of thick fibres in the anterolateral area of the lower thoracic cord is much larger than in other levels.

Chordotomies at a thoracic level show a concentration of ascending and descending degenerated fibres just lateral to the intermediate horn. It might be possible that these fibres, which are mainly of small calibre, connect sympathetic central nuclei of different segments with each other.

The more caudal the level, the larger we may assume the percentage of propriospinal fibres to be. Besides this, all well-known long systems contain large numbers of propriospinal fibres between their own fibres.

In the sacral and coccygeal segments only a small number of fibres can be defined as belonging to long ascending and descending systems. The other ones are propriospinal fibres. It seems probable that thick fibres are more numerous in the periphery and thin ones in the centre of the white matter.

Normal fibres occurring between two ipsilateral hemichordot-

omies were studied in cats H 2875, H 2706, H 2761, H 2807 and H 2816. These fibres were especially easy to locate in the long-survival period specimens (H 2875). In these cats the fasciculus proprius already showed a large amount of normal fibres at a very short distance from a hemisection (Plate 27, fig. 2). The fibres measuring one to two μ in diameter could be seen to arise everywhere directly from the grey matter. They were most conspicuous ventral and lateral to the anterior horn and along the intermediate horn, medial to the lateral pyramidal tract area. At a larger distance from a hemisection normal fibres of small sizes were found entering the more peripheral parts of the white matter and the fasciculus proprius became thicker. Finally, the thin propriospinal fibres occurred even in areas of rather compact fibretracts, such as the lateral pyramidal tract. In cat H 2875, about three to four segments rostral to the lower hemisection, such fibres were present everywhere in the white matter of the anterior and lateral funiculi, with the exception of the area of the dorsal spinocerebellar tract (Plate 27, fig. 3 and 4). In the anterior funiculus thick fibres were also found to be present at some distance rostral to the lower hemisection and originating in the grey matter between the lesions (Plate 27 fig. 2). These are probably fibres belonging to the long ascending systems. Many of these fibres crossed in the anterior white commissure and some could be traced to their destination in an ascending system at the periphery of the lateral funiculus.

CHAPTER 5.

SURVEY OF THE FIBRESYSTEMS OF THE SPINAL CORD.

A survey of the fibresystems occurring in the cord of the cat will be given, together with peculiarities about their fibre content and interrelations. A number of levels will be described in which the fibre structure can be considered to be typical for that special part of the cord. In order to picture the changes, taking place at the transition of the medulla and the cord, lower medullary levels will also be reported upon.

Mid-olivary level.

Fibresystems are located either along the periphery or along the raphe of the medulla. The pyramids show conspicuously as separate well-circumscribed bundles at the ventral periphery, on both sides of the midline.

Immediately dorsal to them the medial lemniscus can be distinguished, extending more in a mediolateral direction than in a ventrodorsal one, as it does in man. Its medial part is found at both sides of the midline between both inferior olives, its middle part lies between the olive and the pyramid and its lateral part surrounds the olive peripherally and laterally. Thus, the inferior olive is entirely surrounded by the medial lemniscus, with the exception of its dorsal surface.

In the area lateral to the medial lemniscus, nervefibres of small dimensions can be distinguished when one uses high power magnification. They are continuous with the spinoreticular fibres lying ventromedially in Gowers' tract in the cord. They are scattered among reticular elements and, in fact, constitute part of the reticular formation. These fibres probably mediate pain impulses. They terminate however, in the reticular formation in a level somewhat rostral to the present one.

Lateral to this small-fibred area the thick fibres of the ventral spinocerebellar tract are found. They are not numerous because many fibres, contained in G o w e r s' tract in the cord, terminate in the lateral reticular nucleus. External arcuate fibrebundles pass between them and divide them into separate bundles. Dorsolaterally the tract gradually merges into the rubrospinal tract area and therefore, a sharp border-line can not be distinguished between these two tracts.

The rubrospinal tract area is separated from the surface of the medulla by external arcuate fibres and within it reticular formation elements are rather numerous. The area has a triangular shape, the base towards the surface and the apex directed medially into the reticular formation. Besides thick rubrofugal fibres many smaller ones are found in it, for the greater part presumably of reticular formation origin. Dorsolateral to this area a small number of fibres of the dorsal spinocerebellar tract are found. The other ones have already shifted dorsally into the restiform body, where they assume a dorsomedial position.

Medial to the ventral half of the restiform body, one finds the descending branch of the fifth nerve, a crescent-shaped compact body of fibres. The nucleus lies at its medial side.

In the centre of the medullary tegmentum, within the reticular formation, scattered thick fibres represent the direct lateral vestibulospinal tract. They are found in a rather large area, extending from about the central part of the medial longitudinal fascicle to the lateral ti pof the medial lemniscus. These vestibulospinal fibres do not form a tract since the fibres are widely scattered and many foreign reticular elements occur among them.

Dorsally, on both sides of the raphe, the medial longitudinal fascicle is present, and extends to touch the floor of the fourth ventricle. Its medial margin is rather sharp and regular but its lateral margin is corrugated and very vague.

In some places areas of thin fibres, presumably reticulospinal, can be found entering it. Laterodorsal to the fascicle many scattered thick fibres are present. They are mostly vestibulospinal fibres, on their way to join the fascicle, mixed with a few reticulospinal ones, that will either stay in the reticular matter

or join the fascicle also. In the foregoing chapter the location of the constituant fibres of the fascicle has been described.

Dorsal to the olivary complex no circumscribed areas of fibres can be distinguished. Scattered fibres, belonging to either the medial longitudinal fascicle or the reticular formation proper, are the only ones present.

Low-olivary level. (Plate 2).

This is the level where the fourth ventricle narrows to the central canal of the cord. The pyramids are still uncrossed and situated ventrally. Dorsal to them the decussation of the medial lemniscus is conspicuous and obliquely cut lemniscal fibres are seen between the pyramid and the olive.

Ventral to the olive two kinds of fibres are found, medially there are fibres of the medial lemniscus and laterally those of the cervico-olivary tract. The latter fuse with the direct vestibulospinal fibres at their lateral aspect.

Deiters' direct vestibulospinal tract has shifted ventrally and touches the pia mater. It is much more compact than in the foregoing level, with the exception of its dorsomedial tip which merges into the reticular formation. A few fibres of the spinoreticular system can be found lateral to the vestibulospinal tract, the majority of them, however, is scattered throughout the reticular formation. The lateral reticular nucleus is very large at this level and many spinoreticular fibres are scattered throughout it.

The ventral spinocerebellar tract and the rubrospinal tract are found in approximately the same position as in the previous level. The area of the latter is rather large because of the fact that many reticular formation elements are present among its fibres.

Dorsal to the rubrospinal tract, fibres of the dorsal spinocerebellar tract become more numerous, although many of them are still found laterodorsally on their way to the restiform body. They seem to pass through a nucleus situated lateral to the rubrospinal tract. *It might be possible that some of the dorsal spinocerebellar fibres terminate there.*

The descending branch of the trigeminal nerve has decreased in size. Dorsal and dorsomedial to it the posterior funicular nuclei can be found. The medial longitudinal fascicle is still found on both sides of the raphe but its most ventral fibres have shifted laterally to a position dorsal to the caudal portion of the inferior olivary complex. Most of these fibres are thick reticulospinal fibres, mixed with some tectospinal ones. The reticular formation proper has decreased in size and lies in the centre of the medullary tegmentum, lateral to the medial longitudinal fascicle.

The level of the pyramidal decussation.

In this level both the pyramidal decussation and the transition of the medulla to the cord are found. As both are not completed in one level only, the changes which occur will be described in a high, a middle and a low level of decussation.

In the course of this description the order of the different parts discussed will be reversed to a dorsoventral one.

The high pyramidal decussation level. (Plate 3).

In the high level both pyramids are still found at the ventral aspect of the cross-section, where their dorsal fibres enter the decussation. Decussation occurs in separate bundles that traverse the medial longitudinal fascicle in its dorsal part and subsequently proceed through the reticular formation to the posterolateral funiculus. Many fibres of the pyramidal tract, however, terminate in the reticular substance at the base of what will be the posterior horn in a more caudal level. This reticular substance lies medial to the nucleus of the descending branch of the trigeminal nerve. Other pyramidal fibres terminate in that ventrolateral part of the ventral reticular substance, that more caudally will be the anterior horn. *Apparently only about 50—60 percent of the crossing fibres reach the posterolateral funiculus.*

Cervico-olivary fibres are found ventrolateral to the ventral pyramid. Their fibre calibres are unchanged and measure from about 3—5 μ. The medial longitudinal fascicle is found lateral and dorsolateral to the crossing pyramidal bundles. Its lateral

margin is very vague and merges into the ill-defined antero-lateral area of the white matter. Between the medial longitudinal fascicle and the pyramidal crossing the small fascicle of obliquely cut fibres of the crossing cervico-olivary tract is found. Its fibres partly intermingle with the crossing pyramidal fibres. Ventrally, the fibres of the medial longitudinal fascicle extend far laterally and almost fuse with those of the vestibulospinal tract.

The vestibulospinal tract is located lateral to the area of the cervico-olivary tract. Its area is more or less hornlike in shape because its lateral part protrudes dorsolaterally into the white matter of the anterolateral funiculus. Its area is characterized by the presence of very thick fibres, mixed with large numbers of much smaller ones. Peripheral to the most lateral part of this area fibres are much smaller in diameter. They belong to the spinoreticular system, which participates in the formation of G o w e r s' anterolateral ascending fascicle. The part occupied by spinoreticular fibres can not be distinguished because their fibre sizes do not differ from those within the anterolateral area. In the foregoing paragraph they were described as terminating partly in the lateral reticular nucleus. In this "high" level the spinoreticular fibres constitute an ill-defined peripheral strand of fibres which widens dorsolaterally and part of them lies already in the caudal pole of the lateral reticular nucleus. Dorsally, the area merges into the ventral spinocerebellar tract area without a noticeable border-line.

This last area forms the wider part of the peripheral strand of ascending fibres in the anterolateral funiculus. In this strand fibre sizes decrease in a ventromedial direction. The homogeneous nature of the strand decreases in the same way.

The medial border of the dorsal spinocerebellar tract can not be defined in normal cases because the diameter of its fibres approximately equals that of the adjacent rubrospinal fibres. When degenerated, however, this border proves to be rather distinct, even though some intermingling of fibres of both tracts is apparent. In ascending degeneration specimens the medial border of the dorsal spinocerebellar tract forms a wedge into the rubrospinal tract area, whereas the ventral tract consists

of a bulging just ventral to this triangular area and partly intermingles with it. From this it is obvious that the peripheral strand of ascending fibres is very irregular in shape and that its constituent elements can not very well be separated.

The rubrospinal tract area occupies the greater part of the posterolateral funiculus. Its medial tip touches the reticular formation and its dorsal margin is indicated mainly by crossing pyramidal bundles travelling in a lateral direction. These pyramidal bundles split the grey matter into a "mazy" reticulum of grey and white matter.

The middle pyramidal decussation level. (Plate 4).

In the midline the decussating pyramidal bundles are found, which after their decussation proceed laterally and form the white matter of the reticular formation. Lateral to the ventral pyramidal tract and ventral to the medial longitudinal fascicle, the cervico-olivary fibres are situated in a homogeneous area, underneath the pia mater. Fibres from the medial longitudinal fascicle shift far laterally even into the anterolateral funiculus. This lateral portion of the medial longitudinal fascicle is found between the fasciculus proprius of the anterior funiculus and Deiters' tract. This lateral part consists chiefly of thick and long descending reticulospinal fibres. Although there is no lateral reticular nucleus the rubrospinal and both spinocerebellar tracts have the same topography as in the foregoing level.

The low pyramidal decussation level. (Plate 5).

At the level of exit of the first cervical root the pyramidal fibres cross together with the cervico-olivary fibres which they resemble very much. The cervico-olivary fibres shift first medially and subsequently dorsally, underneath the pia mater, toward the commissure. In this way the medial longitudinal fascicle is completely separated from the outer surface of the cord by cervico-olivary fibres. The arrangement of the constituents of the white matter is that of the cord. Ventral to the posterior horn a reticular area is found in which most pyramidal fibres are situated and many apparently terminate. The lateral cervical

nucleus gradually separates from the reticular formation and takes its site in the middle of the posterolateral funiculus, surrounded by pyramidal fibres.

The first cervical segment. (Plate 6).

The pyramidal tract has shifted entirely into the posterolateral funiculus at this level, separating the dorsal spinocerebellar and the rubrospinal tract. A few bundles penetrate laterally and reach the surface, dividing in this way the superficial strand of ascending fibres into a dorsal and a ventral part.

The neck of the posterior horn is narrow and lateral to it a reticular area is found which contains thin fibres. The exact nature of this fibres has not yet been determined since in chordotomies degeneration is very incomplete. Possibly a number of the fibres present here will descend with the lateral pyramidal tract.

The lateral cervical nucleus is found in the centre of the lateral pyramidal tract. Small fascicles of fibres connect it with the dorsal spinocerebellar tract. This tract lies in the uttermost dorsal part of the posterolateral funiculus. Only a small processus, tapering in a lateral direction, is present along the laterodorsal margin of the funiculus. Degenerated fibres of the dorsal spinocerebellar tract can be traced into the lateral cervical nucleus and be seen to terminate around its neurons. From this nucleus axons can be followed to the anterior commissure, where they cross to form the cervico-olivary tract.

The rubrospinal tract keeps its triangular shape. It lies immediately ventral to the lateral pyramidal tract area, but part of its fibres are contained in the pyramidal tract. Presumably, rubrospinal fibres are confined to the thick ones occurring in its area, whereas the numerous smaller ones originate in levels caudal to the mesencephalon, mainly in the medullar reticular substance. A few of its fibres lie in the lateral part of the pyramidal tract. These fibres can not be distinguished in normal specimens from spinocerebellar ones, which are also present and have similar sizes.

The wedge-shaped area of ascending fibres, protruding into

the rubrospinal tract area, has slightly decreased in size. The fascicle of ascending fibres in the periphery of the anterolateral funiculus, not belonging to the ventral spinocerebellar tract, is also of smaller size than in the previous level. This may be attributed to the fact that many of its fibres lie scattered between the fibres of the anterolateral area, from which they do not differ much in size, and from which they can only be distinguished with difficulty.

The direct vestibulospinal tract has kept its hornlike shape and the spinoreticular fibres border it ventrolaterally. The anterior funiculus, for the greater part, is occupied by the medial longitudinal fascicle which is separated from the pia mater of the anterior medial fissure by the cervico-olivary fibres. Dorsal to the vestibulospinal tract the medial longitudinal fascicle fibres tend to shift laterally and disperse among the fibres of the anterolateral area proper. The groups of fibres found between the fibres of the anterior commissure, apparently constituting the most dorsal part of the medial longitudinal fascicle, do not belong to it, since they do not partake in its degeneration after severance of the fascicle in the medulla. The lateral margin of the fascicle is very indistinct. Its fibres get gradually less numerous there and are replaced by propriospinal fibres of similar sizes. Besides this, fibres originating from the spinal grey matter pass through the fascicle on their way to some tract area at the periphery of the cord.

The second cervical segment. (Plate 7).

The pyramidal fibres, which interrupted the peripheral strand of ascending fibres in the foregoing level, start to recede to the lateral pyramidal tract proper, and consequently this strand is continuous again at the lower part of C_2 segment. It is wide at the dorsalmost part of the posterolateral funiculus where the dorsal spinocerebellar tract has its site; it is somewhat less wide ventrolateral to the rubrospinal area, where the ventral spinocerebellar tract is located. Lateral to both the pyramidal and the rubrospinal tract this strand is rather narrow. The fibres, constituting this strand, are composed of those from both

spinocerebellar tracts, fibres of the dorsal tract extend lateral to the rubrospinal area for a small distance.

The lateral cervical nucleus, within the lateral pyramidal tract area, finds its termination at about the lower end of the second cervical segment. It is spindle-shaped, the longer axis running from dorsolateral ventromedially. From its medioventral part efferent fibres emerge and at its dorsolateral part afferent fibres enter. Medial to it, within the posterior horn, a small reticular area is still present which, proceeding caudally, rapidly decreases in size. The fibrebundles contained in this reticular area are possibly found in more caudal levels in the white matter, between both horns, adjacent to the grey matter.

The fasciculus proprius of the cord comes into being at the level of the pyramidal decussation and gradually increases in size at lower levels. At this level it is very narrow in the anterior funiculus, much wider around the ventral and the lateral aspect of the anterior horn and narrow again between both horns. Lateral to the posterior horn it is almost non-existent. The anterolateral area does not show any distinct circumscribed fibretract and increases in size as one proceeds down the cord. In both structures thick fibres are rare, as are long fibres, since fibre degeneration after chordotomies hardly ever exceeds 4—5 segments in length. Longer ill-defined fibres presumably take a more peripheral course, hidden somewhere near or within the long well-known systems.

The third cervical segment.

This segment shows the typical spinal cord arrangement of its fibresystems. Although the maximum number of spinal cord fibres is present in the first cervical segment, the typical arrangement is not found there because of its close proximity to the medulla. The spinal topographical pattern can be found typically only in the third segment and essential changes will no longer be encountered throughout the more caudal part of the cord. In the cross-section of normal specimens thick-fibred tracts can be readily distinguished because of their red hue, which is due to the fact that myelin of thick fibres stains more brilliantly

red than that of small fibres. Counting fibres of different sizes and determining percentages of them in a given tract may produce a characteristic fibrepattern that, when compared with the figures of percentages of other tracts, may demonstrate striking differences. *Relatively small differences in fibre content, however, can be much more readily seen at high power microscopical examination and from photomicrographs than by comparing the figures of the fibrepattern.* One thick fibre of 10 μ diameter occupies the surface of 25 fibres of 2 μ. From this it will be evident that the importance of a small percentage of thick fibres is less striking in terms of its number than in terms of the optic impression given by a fibresystem. At this level all fibres of the lateral and anterior funiculus were measured and counted and the fibrepatterns of the circumscribed tracts were computed. The fibrepatterns, in this level and the following ones, have been counted by B. Matricali, a student working with us.

The *dorsal spinocerebellar tract* contained about 10—12,000 fibres, divided among the following groups of sizes: (Diameters include the myelin sheath.)

Smaller than 1½ μ 10 %; 1½—3 μ 28 %; 3—5 μ 27 %; 5—10 μ 21 %; 10—15 μ 10 %; over 15 μ 3 %. Thick fibres seem to be rather unimportant numerically, nevertheless they are very conspicuous because they are much larger than the thin ones. A relatively small number of thick fibres occupies the larger part of the surface-area of a tract. When one third of the fibres are over 5 μ in diameter a tract becomes conspicuous because of its thick fibres (Plate 18, fig. 2).

In the *ventral spinocerebellar tract* the figures were: total amount 10,000; percentages 21 %; 47 %; 17 %; 8 %; 4 % and 2 %, respectively. This tract does not differ from the mean distribution of fibres of different sizes in the cord. It is distinguishable, however, by the presence of fibres over 15 μ in size (Plate 21, fig. 1).

In the *spinoreticular tract* figures were: 3,000; 24 %; 37 %; 24 %; 9 %; 3 % and 2 %. Here the small fibres predominate and the thick ones present may belong to either the ventral spinocerebellar or the direct vestibulospinal tract, because con-

siderable intermingling occurs in this area (Plate 20, fig. 4).

The *lateral pyramidal tract* is characterized by totally different figures: the total amount of fibres was 32,000, percentages were 26 %; 52 %; 14 %; 4 %; 2 % and 0.8 %. Fibres less than 5 μ in diameter amount to over 90 % of the total number, which makes it a thin-fibred tract (Plate 22, fig. 3). This is even more evident than the figures imply, since part of the very thick fibres belong to the rubrospinal tract. Part of the smaller fibres however, are not corticospinal fibres but have joined the tract caudal to its decussation.

The *rubrospinal tract* resembles the lateral pyramidal tract with regard to its fibrepattern, its figures were: total number 15,000, percentages 20 %; 55 %; 15 %; 5 %; 1.5 % and 2.5 %. This tract is also thin-fibred, but experiments showed that the majority of the thin fibres do not belong to the rubrospinal system, which therefore is a thick-fibred system. Thickest fibres were more numerous in it than in the lateral pyramidal tract, representing 2.5 and 0.8 % respectively. This is the reason that the rubrospinal tract is optically completely different from the lateral pyramidal tract (Plate 24, fig. 2). Therefore, it would be better not to speak of the pattern of the rubrospinal tract, for only the thick fibres are rubrospinal. The pattern given is of the area wherein rubrospinal fibres occur, which is quite another thing than the pattern of the rubrospinal tract.

The same remarks can be made about the *direct vestibulospinal tract*. Figures were: total amount about 7—8,000; percentages 23 %; 36 %; 19 %; 11 %; 8 % and 3 %. Only the thick fibres originate from the vestibular nuclei, not exceeding the 1500 fibres, whereas the smaller ones are of reticular origin and gradually become replaced by propriospinal fibres in lower levels (Plate 26, fig. 3).

The *medial longitudinal fascicle* is very heterogeneous. Its thick fibres make it stand out against the reticular formation in the medulla. The total number was 15—18,000; percentages were 12 %; 24 %; 51 %, 5 % and 4 %. Thickest fibres over 10 μ in diameter are chiefly of vestibular or tectal or interstitial origin (Plate 25, fig. 2). The smaller fibres, beyond doubt, are

of reticular origin. This was demonstrated in the medulla in a few experimental animals.

The area between the medial longitudinal fascicle and Deiters' tract contained a relatively large amount of thick *reticulospinal fibres*. Its spectrum has been established separately therefore. The figures were: total amount from 3,000—4,000; percentages 28 %; 38 %; 17%; 8 %; 4.5 % and 4.5 %. The thin as well as the intermediate fibres are distributed as they are in the direct vestibulospinal tract, whereas the thick fibres have a distribution as in the medial longitudinal fascicle. From this it will be clear that we deal with a transitional area, between the fascicle and Deiters' tract.

The *cornumarginal area or fasciculus proprius* is characterized by its large amount of thin fibres, its figures were 19 %; 45 %; 25 %; 8 %; none; none. Thickest fibres did not surpass 10 μ in diameter ,with the exception of an occasional thick fibre. The pattern proved to be rather unchanged in lower spinal levels.

The ill-defined area of the anterolateral funiculus showed a similar pattern, except that large fibres were more numerous. Percentages were 21 %; 31 %; 31 %; 10 %; 3.5 %; and 2 %. The thick fibres, here as well as in the fasciculus proprius, may be considered to consist chiefly of those of the long tracts on their way between the central grey matter and their tract area at the periphery of the cord. This anterolateral area will not considerably change its pattern in lower spinal levels. The topography of the third cervical segment may now follow.

The dorsal spinocerebellar tract is located in the dorsalmost part of the posterolateral funiculus. Medially it touches the posterior horn, ventrally it intermingles somewhat with the lateral pyramidal tract fibres and laterally it tapers into a narrow strand of fibres along the surface of the posterolateral funiculus, peripheral to the lateral pyramidal tract. The medial margin of this strand is irregular and vague and its width varies with different animals. Thin fibres are more numerous in it than in the dorsal part of the dorsal spinocerebellar tract. More ventrally, the number of thin fibres immediately increases when the main portion of the ventral spinocerebellar tract is reached.

From this description it is obvious that there is no sharp borderline between both spinocerebellar tracts. They are connected by the peripheral strand of fibres which has been called "*the intermediate spinocerebellar tract*" by Pellizi (92). Most of its fibres, however, enter the cerebellum with the dorsal tract via the restiform body.

The ventral spinocerebellar tract lies wholly within the anterolateral funiculus. Most of its fibres are located closely ventral to the rubrospinal tract area, intermingling considerably with its fibres. The medial border of its dorsal part lies more medially than that of its ventral part. This border is ill-defined and gradually merges into the anterolateral area which does not contain any known fibresystem. Ventromedially the tract merges into the spinoreticular system, fibres of which are also located in the ventral spinocerebellar tract and medial to it. Lamellation is conspicuous only in the mid-cervical part of the dorsal spinocerebellar tract, where fibres from cervical segments are found, lying medially to those originating from lower levels of the cord. The ventral tract does not show such lamellation clearly. Fibres from the cervical intumescence mostly travel separately in the anterolateral area and, only gradually, join the tract rostrally where they lie scattered between those from lower levels.

The lateral pyramidal tract is situated in the centre of the posterolateral funiculus, surrounded dorsally and laterally by spinocerebellar fibres. Medially it is separated from the posterior horn by a small bundle of propriospinal fibres, a bundle which immediately gets thicker ventrally, between both horns. In the lateral part of the lateral pyramidal tract rubrospinal fibres are relatively numerous. In its dorsal part they occur so far medially that they touch the posterior horn.

The majority of the rubrospinal fibres is found ventrolateral to the lateral pyramidal tract, but stray fibres can be seen medial to the ascending peripheral strand of fibres all along the lateral margin of the posterolateral funiculus. Everywhere, between the thick rubrospinal fibres, large numbers of smaller fibres are present. A rubrospinal tract, in the classical sense, therefore, can not be found in this segment.

Medial to the peripheral ascending fibres in the anterolateral funiculus other spinoreticular fibres, belonging to either the spinocerebellar or the spinoreticular pathways, are present, dispersed among fibres of a different character, presumably chiefly propriospinal in nature. Otherwise, the anterolateral area consists of fibres which show either ascending or descending degeneration only over a few segments when severed. They, therefore, are to be looked upon as propriospinal fibres, surpassing somewhat those of the cornumarginal area in length. Afferent visceral fibres, as well as intraspinal sympathetic ones, which are considered to be found in the anterolateral area and dorsally in the cornumargina area, can not be distinguished, either in the normal specimen by their fibrepattern or by degeneration after experimental transverse lesions. They may be present, but possibly they either consist of short fibres, forming a frequently interrupted system, or they are contained in the area of known fibretracts and blend with their fibres.

The anterior funiculus consists, for the greater part, of the medial longitudinal fascicle which is very heterogeneous. Its most dorsal part consists of intraspinal fibres, lying immediately ventral to the anterior commissure. Ventral to them the thick interstitiospinal fibres are present, together with vestibulospinal ones originating from the descending nucleus. More ventral both the crossed and the uncrossed fibres from the medial and the lateral vestibular nuclei, mixed with some tectospinal ones, find their site, whereas the other tectospinal fibres lie in the most ventral part of the fascicle. Scattered between the thick fibres mentioned, there are large numbers of smaller ones, chiefly reticulospinal fibres.

Laterally the fascicle is only vaguely circumscribed, as its bundles are gradually replaced by those of the cornumarginal area. Thick fibres in this transitional area are relatively numerous. They may consist chiefly of long tract fibres on their way between the anterior white commissure and the peripherally lying tract they belong to. Within the ventral part of the anterior funiculus the medial longitudinal fascicle extends almost as far laterally as the border-line between the anterior

and the anterolateral funiculus. This lateral part consists of fibres proceeding from the fascicle to their destination somewhere in the ventral grey matter, of part of the tectospinal fibres, and of thick reticulospinal fibres.

The vestibulospinal tract is found ventral to the lateral extension of the medial longitudinal fascicle, bordering the ventral surface of the anterior funiculus. Only its thick fibres are vestibular in origin. Between them relatively large amounts of smaller reticulospinal fibres are present. The tract is traversed by ventral root fibres which make its texture still less compact.

Underneath the pia mater of the anterior funiculus small groups of thin fibres are visible, occasionally mixed with thicker ones from the medial longitudinal fascicle and the direct vestibulospinal tract. The thin fibres belong either to the spinoolivary system or to ascending propriospinal connections.

The fourth cervical segment. (Plate 8).

Its gross fibre structure is essentially similar to that of the previous segment. Only minor changes are noticeable.

The main dorsal portion of the dorsal spinocerebellar tract is almost totally separated from the ascending fibres lying peripherally to the rubrospinal tract, since only a few of such fibres are present lateral to the lateral pyramidal tract area. Lateral to the rubrospinal tract area such fibres are moderately numerous. They merge ventrally into the ventral spinocerebellar tract. The latter tract is only compact in its dorsal and peripheral part, otherwise its fibres are intermingled with those of the rubrospinal tract and are even found medial to its ventralmost fibrebundles.

Spinoreticular fibres can be found ventral to the ventral spinocerebellar tract within a large area which reaches the lateral tip of the vestibulospinal tract. Descending fibres are found in small numbers in the most medial part of the tract of Gowers. They, presumably, originate from the medullary reticular formation. This spinoreticular area, therefore, does not differ essentially from the anterolateral area where ascending and descending fibres are also mixed.

The rubrospinal and the lateral pyramidal tract present no changes.

The direct vestibulospinal tract extends into the anterolateral area, whereas medially it almost touches the ventral tip of the anterior funiculus. Scattered fibres, having left the vestibulospinal tract, lie dorsal to it in the ill-defined part of the anterior funiculus, presumably on their way to their termination somewhere in the ventral grey matter.

The medial longitudinal fascicle shows no appreciable changes.

The sixth cervical segment. (Plate 9).

Spinocerebellar fibres, situated lateral to the rubrospinal tract, have considerably increased in number. They bulge into the rubrospinal tract area. Dorsally they are in connection with the main portion of the dorsal spinocerebellar tract and ventrally they merge into the ventral spinocerebellar tract. The ventral spinocerebellar tract area extends medial to that of the rubrospinal tract and fibres of both systems intermingle. The ventral border of the ventral spinocerebellar tract can not be determined because many of its fibres are mixed with the spinoreticular fibres, lying ventromedial to it.

The pyramidal tract has decreased in size, due to the fact that part of its fibres have reached their destination in the grey matter. It is not obvious that the medially situated fibres have left it. Experimental results point to the conclusion that the pyramidal fibres to the cervical cord are scattered among the fibres with a different destination.

Rubrospinal fibres are found all over the pyramidal area, even in its most medial part, although the majority are found in its lateral half. A few rubrospinal fibres lie amidst the spinocerebellar fibres, lateral to the rubrospinal tract area. Most of them however, are assembled in the area ventrolateral to the pyramidal tract area.

Within the direct vestibulospinal tract thick fibres are becoming rare since vestibulospinal fibres have, for the greater part, left it. The tract is indicated only by small numbers of thick fibres, along the ventral border of the anterior funiculus,

encroaching somewhat upon the anterolateral funiculus. Lateral to it, both peripherally and centrally, spinoreticular fibres are present.

The medial longitudinal fascicle, apparently, is unchanged but experiments showed many of its fibres to be of spinal origin. Dorsally, a few interstitiospinal and ventromedially some tectospinal are present in it. Most of the thick fibres, however, are of vestibular origin. These fibres keep their original position to some extent but they are more scattered than in the fourth cervical segment. Thick reticulospinal fibres are still present in the area between the direct vestibulospinal tract and the centre of the medial longitudinal fascicle. Spino-olivary fibres are found underneath the pia mater of the anterior funiculus.

The eighth cervical segment. (Plate 10).

This segment lies caudal to most of the cervical intumescence and the fibres which originate or terminate in this enlargement become few in number. The figures of the fibre content of the different tracts will show this change in a striking way as will be seen below.

The *dorsal spinocerebellar tract* contained as many fibres in C_8 as in the C_3 level viz. between 10.000 and 15.000. Percentages were 11 %; 42 %; 12 %; 9 %; and 1 %. Thick fibres have diminished in percentages, thin ones increased. The tract resembles more the other spinal cord tracts. Comparing these numbers with those of C_3 it seems that thick fibres are added to the tract in more rostral cervical levels, a fact which has been confirmed by experiments. Furthermore, foreign fibres certainly have penetrated into the area, increasing the amount of thin fibres. This might be due to the shift of the spinocerebellar fibres into an area, lateral to the rubrospinal area, where more thin fibres occur.

The most homogeneous part of the dorsal spinocerebellar tract is found right in the dorsal part of the posterolateral funiculus, dorsal to the lateral pyramidal tract area. The number of fibres there, however, is much less than in higher levels. This has

to be attributed to the shift of many fibres into a triangular field, lying lateral to the rubrospinal tract area. The most dorsal part of the tract can be considered to contain especially the fibres going to the lateral cervical nucleus, whereas the majority of the spinocerebellar fibres lies more ventrally. Fibres, joining the tract in the 7th, 6th and 5th cervical segment, come to lie ventral to the dorsal part before intermingling with the fibres from lower segments, already present in it. In the rostral spinal segments the ventral fibres shift dorsally, but only partially, since a number of them keep their position at the lateral aspect of the posterolateral funiculus.

The *ventral spinocerebellar tract* can not very well be circumscribed since many of its fibres are dispersed in the anterolateral funiculus. Only its dorsolateral main portion could be counted, the total number of fibres was 3,000; percentages of fibres of different sizes were 20 %; 34 %; 23 %; 13 %; 6 % and 3 %. These figures only account for the compact homogeneous part of the tract. More fibres are present in a scattered fashion.

Spinoreticular fibres can not be counted because they are too dispersed.

Ventral spinocerebellar and spinoreticular fibres form a narrow band just underneath the pia mater of the anterolateral funiculus, the remaining fibres are dispersed more medially in the funiculus between propriospinal fibres. Spinoreticular fibres, however, occur as far ventromedially as the most lateral anterior root fibres.

The *lateral pyramidal tract* has somewhat diminished in size, percentages were 35 %; 38 %; 18 %; 7 %; 1.5 % and 0.2 %. The total number of fibres was the same as in the C_3 segment, therefore, thick pyramidal fibres have diminished more than the figures indicate. *The thick pyramidal fibres, therefore, are not projecting especially to the lower parts of the cord.* That thin fibres are present in numbers larger than previously should be attributed chiefly to foreign fibres which join the tract. The tract is localized in the centre of the posterolateral funiculus separated from the surface by spinocerebellar fibres, from the

posterior horn by a bundle of propriospinal fibres, which has already been described in the C_3 segment.

The *rubrospinal tract,* containing both pyramidal and ventral spinocerebellar fibres, can not be very distinctly circumscribed. Figures, therefore, are not very characteristic. Fibres numbered 8,000 to 10,000 which is only half those in the C_3 segment, percentages were 27 %; 42 %; 20 %; 8 %; 2 % and 0.8 %. Both very thick and thin fibres decreased in numbers, medium-sized ones became relatively more numerous. Thick fibres partially terminated, partially shifted to the pyramidal tract area, and thin fibres possibly were replaced by medium-sized ones.

The *direct vestibulospinal tract* fibres could not be counted, because they are not assembled in a circumscribed area. Thick vestibulospinal fibres lie peripherally at the transition of the anterior and the anterolateral funiculus. These fibres are few in number and the area they occupy is very narrow in a dorso-ventral direction. Some of the fibres are located in the centre of the anterior funiculus, obviously on their way to the grey matter. The border with the medial longitudinal fascicle is rather distinct because the amount of thick fibres abruptly increases there.

The *medial longitudinal fascicle* has not changed its configuration. Only some interstitio- and tectospinal fibres are left. Both do not descend beyond the cervical segments. The various kinds of vestibulospinal fibres are still present, they retain their localization, though they are somewhat more widely scattered. Medium-sized reticulospinal fibres have disappeared and are mostly replaced by descending propriospinal fibres. Lateral and ventral in the area only a few thick reticulospinal fibres have been preserved, they stand out because of their large size. Both the medial and the dorsal border of the ventral part of the fascicle are very vague as its fibres gradually merge into the fasciculus proprius.

The second thoracic segment. (Plate 11).

This is the most caudal extent of the cervical intumescence. Only the fibres to and from the thoracic and lower parts of

the cord are left, and changes in the structure of the white matter are considerable. Most of the tracts have greatly decreased in size and the area devoid of circumscribed tracts is relatively large.

The larger part of the dorsal spinocerebellar tract lies dorsal, the smaller part lateral to the pyramidal tract area. In the first thick fibres, and in the other thin fibres, are more numerous. The pyramidal tract area is round in shape. In its lateral part about one third of the rubrospinal fibres are located. Corticospinal fibres make u ponly about half of the fibre content of the area, rubrospinal ones are few, not surpassing 200 in number and foreign fibres, therefore, are relatively numerous.

The rubrospinal tract area proper has not changed its site, fibres separating it from the outer surface are more numerous than in the previous level. They consist of dorsal spinocerebellar fibres. Degeneration in the areas of both the pyramidal and the rubrospinal tracts is much more marked in a high chordotomy than in a section of the brain stem, which implies that many fibres, descending in these areas, do not belong to the tracts. Their numbers amount to about half of the fibres present in the areas at this level.

The ventral spinocerebellar tract, apparently, is very small and has greatly decreased in size, since many of its fibres are dispersed throughout the peripheral half of the anterolateral funiculus. Very dorsolateral within the anterolateral funiculus the tract seems to be homogeneous, as it consists mostly of thick fibres. More ventral, however, intermingling with afferent fibres to the lateral reticular nucleus of the medulla and other ascending propriospinal fibres is considerable.

In the case of hemichordotomy at C_8 segment, distal to the section, there is an accumulation of degenerated fibres just lateral to the ventral horn, which extends into this Th_2 segment. Possibly, it represents the longitudinal tract interconnecting the thoracic cord sympathetic centres. This tract has been called the intermedio-longitudinal tract. Within the anterior funiculus the medial longitudinal fascicle and the lateral vestibulospinal tract form one body of descending fibres. The latter can be

distinguished from the former by its larger content of foreign, relatively thin fibres, though a sharp border-line between both can not be noticed. The medial longitudinal fascicle consists of vestibulospinal fibres, the last tectospinal fibres, and large numbers of propriospinal fibres. The latter are found chiefly in its dorsal part, though in the main part they are not absent. Underneath the pia mater of the anterior funiculus thin ascending fibres are found in appreciable quantities.

The seventh thoracic segment. (Plate 12).

This segment is more or less a typical thoracic cord segment. Distinguishable fibresystems are limited to the dorsal spinocerebellar, the lateral pyramidal, the rubrospinal tract and the medial longitudinal fascicle. The dorsal spinocerebellar tract consists of a dorsal part extending far mediodorsally to the lateral pyramidal tract and a lateral part lying lateral to it. The former consists chiefly of spinocervical and propriospinal fibres whereas the latter contains the dorsal spinocerebellar fibres, mixed with propriospinal ones. The fibrepattern of each part differs appreciably, the dorsal part contains a larger number of thick fibres, and gradually both parts become entirely different. The dorsal part is located just lateral to Lissauer's marginal zone, the thick spinocervical fibres, therefore, penetrating between the lateral pyramidal tract and this zone.

The lateral pyramidal tract is elliptical in shape, the long axis directed from dorsolateral ventromedially. Because of the presence of the dorsal spinocerebellar tract, the lateral pyramidal tract only occupies the dorsomedial part of the posterolateral funiculus. Many rubrospinal fibres are present in it, together with considerable numbers of propriospinal fibres. The latter are thin and medium-sized, the former are chiefly very thick and are found especially in the lateral part of the tract area.

The rubrospinal fibres are grouped around the medial tip of the triangular area of the ventral part of the dorsal spinocerebellar tract, extending both ventrally and dorsomedially beyond it. Ventrally, rubrospinal fibres can be found mingling with ventral spinocerebellar ones. Thus rubrospinal fibres prove

to be scattered all over the lateral part of the posterolateral funiculus. Most of the fibres within this part however, have nothing to do with the rubrospinal tract, since they are predominantly propriospinal fibres.

The ventral spinocerebellar tract fibres are still large in number, but they are scattered throughout the anterolateral funiculus and a tract is no longer distinguishable. From the outer surface they are separated by thick descending fibres which are probably propriospinal. In a ventromedial direction spinocerebellar fibres become rarer and are replaced by spinoreticular ones which are mostly of smaller sizes. Lateral to these fibres are situated the direct vestibulospinal fibres, mixed with other descending ones. Thick fibres are found especially in the peripheral half of the anterolateral funiculus, its central half being occupied by propriospinal ones of smaller sizes.

The medial longitudinal fascicle still is of ample size, degeneration however, shows that only a minority of its fibres is derived from supraspinal levels. Thick fibres are relatively numerous and chiefly represent vestibulospinal ones. The dorsal half of the medial longitudinal fascicle is totally devoid of supraspinal fibres, though it contains as many thick fibres as the ventral half. The majority of the vestibulospinal fibres, already travelling in the fascicle in the upper cervical cord, is found in the lateral part of the ventral half of the fascicle, touching the anterolateral funiculus. Thin ascending fibres are still present underneath the pia mater of the anterior funiculus.

The vestibulospinal tract, as such, is no longer present, its fibres are scattered among spinoreticular and spinocerebellar ones in the peripheral part of the anterolateral funiculus. The fibres can be found so far dorsally that they lie in the region of the ventral spinocerebellar tract.

The first lumbar segment. (Plate 13).

The lower thoracic and the two upper lumbar segments are almost similar with regard to their fibre structure.

The dorsal spinocerebellar tract has divided into two separate areas which have to be looked upon as two different tracts. The

dorsal one, lying as a cap over the lateral pyramidal tract, consists of propriospinal and spinocervical fibres, predominantly The latter fibres are mostly thick and make the tract very conspicuous because of their large numbers. Those of smaller sizes are propriospinal fibres, but there are also thick propriospinal fibres. Percentages of fibres of different sizes were 17 %: 26 %; 20 %; 18 %; 16 %; 2 %. With the exception of the thickest fibres percentages are almost equal, which is exceptional because usually thin fibres are much more numerous than medium-sized and thick ones.

Ventral to the dorsal part of the dorsal spinocerebellar tract the lateral pyramidal tract is located, it is still elliptical in shape but the long axis has changed to a transverse position. The pyramidal tract touches the pia mater and separates the two parts of the dorsal spinocerebellar system. Its size and fibre-pattern at this level are about equal to those in the midthoracic segment, the former amounts to about half of that at a high cervical level. However, only about 40 percent of the fibres are cerebrospinal, as experiments have demonstrated. The thick fibres are mostly rubrospinal and the thinner ones propriospinal. The latter can not be distinguished from the cerebrospinal fibres by their calibres. They, however, are demonstrated in chordotomies which increase the degree of degeneration in the pyramidal area, the more so the lower the level at which the chordotomy is carried out.

The rubrospinal fibres are found chiefly in the lateral part of the pyramidal tract area, where they cause thick fibres to be relatively more numerous than in the medial part.

The ventral part of the dorsal spinocerebellar tract, the only one deserving this name, occupies a large triangular area with its top directed to the junction of the posterior and the anterior horn. From Clarke's column thick fibres can be followed into this top. The spinocerebellar fibres intermingle with many other fibres, predominantly ascending and descending propriospinal ones and a few rubrospinal fibres. The dorsal spinocerebellar fibres, in this way, occupy the whole lateroventral half of the posterolateral funiculus.

The ventral spinocerebellar fibres lie scattered throughout the whole dorsolateral part of the anterolateral funiculus. They do not border the surface as they do in higher levels, since at the Th_{10} segment the ventral spinocerebellar fibres are pushed centrally by thick descending fibres that take their site between them and the pia mater. Small numbers of spinoreticular fibres can be seen more ventrally in the anterolateral funiculus.

Direct vestibulospinal fibres are still to be found in the anterolateral funiculus, mixed with the ascending spinoreticular and thick descending fibres.

The medial longitudinal fascicle still is very conspicuous. It shows the same characteristics as it did in the previous level. Its dorsal two third consists of thick descending fibres originating in the cord; only in its ventromedial part numbers of vestibulospinal fibres are present, laterally blending with those of Deiters' tract. Underneath the pia mater flat groups of thin ascending fibres are found, separating the medial longitudinal fascicle from the outer surface of the anterior funiculus. Within the fascicle thick fibres are nearly as numerous as within the dorsal part of the dorsal spinocerebellar tract, part of them are vestibulospinal, the majority are long descending propriospinal fibres.

The fasciculus proprius is very wide, its fibre content is similar to that at higher levels. From the lateral part of the anterolateral funiculus it differs only by its smaller number of thick fibres. The fibres of the fasciculus proprius and anterolateral funiculus may be considered to be similar in character, they are mainly ascending and descending propriospinal ones. Besides these propriospinal ones, fibres passing this area, on their way between the grey matter and their tract at the periphery of the white matter, are relatively numerous at this level.

The fifth lumbar segment. (Plate 14).

This segment lies in the middle of the lumbar intumescence and to some extent is typical for it. The recognizable tracts are the spinocervical-propriospinal tract (the posterior part of

the dorsal spinocerebellar tract), the "lateral pyramidal tract" and the medial longitudinal fascicle.

The most dorsal part of the posterolateral funiculus is occupied by the first-mentioned tract, which at this level consists almost entirely of thick ascending propriospinal fibres, mixed with some spinocervical ones. The fibres of the cornumarginal zone, which extends far dorsally in this segment, are found medial to it.

The ventral part of the dorsal spinocerebellar tract is no longer present as it can not be found below the L_3 segment.

Ventrolateral to the tract described, the "lateral pyramidal tract" area is located. The name of the tract has been set down parenthetically because corticospinal fibres are growing extremely rare in it and do not occur in the next lower segment. Nevertheless, the area is conspicuously degenerated following a chordotomy, the more markedly the lower the section. *Therefore, this area can be considered to consist chiefly of descending propriospinal fibres that descend farther caudally than the cerebrospinal ones.* The latter in this level consist of a very small number of thin fibres not surpassing 100. The thick fibres present are mostly rubrospinal. The other rubrospinal fibres are found lateral and ventral to the pyramidal tract area. They are readily recognized because of their large size. They are the thickest ones present.

Within the anterior funiculus the medial longitudinal fascicle is still conspicuous. It contains many thick fibres, which are mostly propriospinal. The fascicle extends from just ventral to the anterior white commissure along the anterior medial fissure laterally into the ventral and ventrolateral parts of the funiculus.

The vestibulospinal fibres, travelling within the fascicle from the medulla, have shifted medially and it looks as if they reach the grey matter after another shift in a dorsal direction. A few of them are found along the pia mater at the ventral margin of the anterior funiculus. The majority however, lie within the ventromedial tip of the funiculus. Most of the other fibres of the fascicle, thick as well as smaller ones, are descending propriospinal fibres and degenerate only after a hemichordotomy. In

the lateral part of the funiculus a few ascending fibres are scattered among them.

Sacral chordotomy demonstrated the presence of a few ventral spinocerebellar fibres, widely scattered in the anterolateral funiculus.

The cornumarginal area is very large and occupies most of the anterolateral and the larger part of the anterior and the posterolateral funiculi. Thickest fibres are found in its lateral and peripheral portions. Ascending and descending ones are thoroughly mixed. The central part of the cornumarginal area shows the same fibrepattern as one finds in higher levels, in the lateral part thick fibres are more numerous.

The first sacral segment. (Plate 15).

This segment still belongs to the lumbosacral intumescence, it does not differ very much from the previous one. The white matter however, has decreased much in size. The only recognizable tracts are the *dorsal ascending tract* and the *medial longitudinal fascicle*. The pyramidal tract area also can be distinguished but it shows degeneration only after chordotomies, and not after decortication and section of the cerebral peduncle in the midbrain.

The dorsal tract within the posterolateral funiculus shows as a small triangular area, separated form the posterior horn by an area of smaller fibres. Ventrally it is bordered by a propriospinal tract of thin descending fibres, contained in the lateral pyramidal tract area in a higher level. The fibres of the dorsal ascending tract measure from about 10—15 μ in diameter. Lateroventral to it occasionally a single rubrospinal fibre can be found, as rubral ablation specimens show.

The lateral part of the anterior funiculus and the entire anterolateral funiculus do not show any circumscribed area of a special fibrepattern. Only the fasciculus proprius and a more lateral area can be distinguished because in the latter thick fibres are somewhat more numerous than in the former.

The lower sacral and the coccygeal segments. (Plate 16).

The lower levels of the cord can be described together because they are very much alike. The only circumscribed tract is the dorsal thick-fibred ascending tract, consisting of a few spino-cervical and many other propriospinal fibres.

The medial longitudinal fascicle can still be recognized with some certainty. Occasionally a few fibres of supraspinal origin may be encountered in it in these segments.

Just ventral to the dorsal ascending tract thin descending propriospinal fibres are present. Relatively large numbers of thick descending fibres are found along the outer surface of the lateral and the anterior funiculi, with the exception of the most dorsal part of the posterolateral funiculus. Otherwise, the only distinction possible is between a central cornumarginal area with a fibrepattern similar to that in all other levels of the cord, and a peripheral area in which thick fibres are somewhat more numerous. In this latter area long descending propriospinal fibres prevail but a few fibres of long ascending systems also may be present.

CHAPTER 6.

DISCUSSION.

Considering the results obtained with the methylblue-eosin stain, its great advantages are immediately apparent. Fibre-tracts and fibrepatterns are made visible in normal slides and degenerated fibres show almost as well as they do in osmium-stained slides. The use of Häggqvist's technique makes it possible to recognize a tract not only by its localization but also by its fibrepattern, even when the sections of the brain stem or the spinal cord are quite distant from one another. The study of the termination of fibres however, can be better performed with the silver techniques.

A subject in need of some comment is the time necessary for complete degeneration of the severed fibres. According to Lassek it takes twelve months. The thickest axons are the first to show signs of degeneration, the other axons follow between the third and tenth postoperative day. Afteh this time there are no normal axons left in the medullary pyramid, distal to a lesion. Degeneration products of myelin sheaths are found up to one year after section and can be stained until that time (Lassek 1946).

In a recent study (1954) Lance found that pyramidal axons degenerate quickly after being severed. He also found retrograde degeneration, initially up to the first node of Ranvier, and later on up to the first collateral. From our experience it can be said that after 8 days degenerating fibres are conspicuous but fibres start degenerating even a long time after a lesion. For this reason several experiments were repeated and the animal was given a longer survival time than the usual three to four weeks.

THE ASCENDING FIBRESYSTEMS.

The posterolateral funiculus.

It appears that the final word has not been written about the caudal origin of the dorsal spinocerebellar tract. Rothmann (102) found, for the first time, fibres, ascending in this tract, which originated in the sacral segments. The method of abdominal aorta compression, which he used to cause necrosis of the grey matter, seems not very subtle. Much later Beck (5) had the same results, using the more appropriate technique of hemisection. Recently, Chang and Ruch (26) proved the presence of dorsal spinocerebellar fibres from sacral and coccygeal levels in the spider monkey. This animal however, because of its prehensive tail, can not be compared to other mammals. From my experiments it seems that fibres, resembling the dorsal spinocerebellar ones in the cat, are already present in the lowermost sacral segments. The investigators cited were able to trace these degenerated fibres into the cerebellum, whereas in my experiments degeneration did not ascend farther rostrally then the cervical cord and most of the fibres had already terminated in the thoracic cord. Verhaart (115) noticed these fibres, because of their large diameter, and considered them to be dorsal spinocerebellar in nature, but it will be shown that they are of a different character.

Brodal and Rexed (20) found fibres ascending in the dorsolateral funiculus from all levels of the cord to the lateral cervical nucleus. Grundfest and Carter (50) recently demonstrated, by physiological means, the presence of second neuron sensory fibres in the same area, conveying cutaneous impulses to the contralateral inferior olive. According to them these fibres were of large size and crossed in a high cervical level. It is readily conceivable that the fibres present in the utmost dorsal part of the posterolateral funiculus of the sacral segments are the fibres which presence has been indicated by Brodal, as well as by Grundfest. This appears more probable when considering the difference in location of these fibres compared to those originating from the caudal part of

Clarke's column. The latter fibres, initially, are scattered in an area ventrolateral to the pyramidal area, whereas the more caudally originating fibres immediately assume a position at the most dorsal tip of the posterolateral funiculus. Only in the course of their ascent do the real dorsal spinocerebellar fibres join the fibregroup, already present dorsally in the funiculus. The propriospinal, the dorsal spinocerebellar and the cutaneous spinocervical fibres probably intermingle thoroughly, since fibres terminating in the lateral cervical nucleus can be seen to come from all parts of the cross-surface of the dorsal spinocerebellar tract, except from the most lateroventral part.

However, not all of the fibres, present in the posterolateral funiculus of the lumbosacral segments, terminate in the lateral cervical nucleus, since degenerated fibres arriving in the cervical cord, after a midlumbar chordotomy, are much less numerous than in the first lumbar segment. Many of these fibres terminate in the thoracic cord, presumably subserving the same function as the fibres to the lateral cervical nucleus. They probably end in the posterior horn, from where tertiary sensory fibres ascend to higher levels. These tertiary fibres may be assumed to terminate in the contralateral inferior olive, as do the spino-olivary fibres of Brodal, Walberg and Blackstad (22).

The existence of spino-olivary fibres is a subject of much controversy (Ranson and Clark, Mettler, etc.). Brodal et al. (22) demonstrated their existence in the cat, although they were not very numerous. My experiments proved their existence conclusively in the anterior funiculus, underneath the pia mater of both the anterior medial fissure and the ventral side of the anterior funiculus. No matter where a hemichordotomy is performed, small groups of thin degenerated fibres, one to three μ in diameter, are found at these sites. In this way they can be considered to constitute a system comparable to that of the efferent fibres of the lateral cervical nucleus. This assumption, however, needs further substantiation as I was not able to repeat the experiments of Brodal, Walberg and Blackstad (22). The only terminal degeneration in the inferior olives which I was able to demonstrate was after a hemichordot-

omy at the second cervical segment, which destroyed part of the lateral cervical nucleus. The efferent fibres of the lateral cervical nucleus also lie in the contralateral anterior funiculus and terminate in the caudal parts of the inferior olivary complex.

The lowermost part of Clarke's column is situated at the transition of the 2nd and the 3rd lumbar segment. From that level upwards into the thoracic cord many fibres from this nucleus penetrate into the homolateral posterolateral funiculus. I was not able to demonstrate crossed fibres in the dorsal spinocerebellar tract as did Pass (91). Grundfest and Campbell (49), as well as Morin and Haddad (83), demonstrated crossed fibres in the tract by physiological means. It is extremely difficult to sever only one dorsal column and encroachment upon the other probably was the cause of Pass' results. The silvernitrate, injected into the column of Clarke, probably diffused somewhat into the contralateral column. A midline incision through the posterior grey commissure certainly will destroy the medial part of both Clarke's columns, as is demonstrated in the experiments on the cats H 2601 and H 2725. Therefore, I am of the opinion that Yoss' studies (128) on primates are more in accordance with my results. Yoss also found the fibres to be located ventral to the pyramidal tract in the lower parts of the cord.

In none of my slides crossing fibres could be seen in the posterior grey commissure, with the conclusion that there is no commissure at all in the cat. It still has to be explained why in physiological experiments on the dorsal spinocerebellar tract both crossed and uncrossed connections often are found.

The following concept of the afferent sensory system in the posterolateral funiculus is offered. Primary proprioceptive fibres in the posterior funiculus, medial to the posterior horn, ascend to the upper lumbar segments where they terminate around the cells of Clarke's column. The secondary proprioceptive neuron-axons take a position at the ipsilateral half of the cord, initially ventral to the pyramidal tract and afterwards right at the dorsal part of the posterolateral funiculus. They reach the cerebellum via the restiform body.

The primary afferent cutaneous fibres terminate immediately after their entrance into the posterior funiculus or give off a collateral to the relay nucleus, which is probably situated at the base of the posterior horn. The secondary sensory neuron-axons immediately take a position extremely dorsal in the homolateral posterolateral funiculus. Fibres are added to them at all levels, but nowhere in great masses, as in the dorsal spinocerebellar tract at both ends of Clarke's column. Part of the secondary sensory neuron-axons again terminate somewhere in the posterior horn and the post-synaptic fibres probably ascend in the contralateral anterior funiculus to the inferior olive. The remainder of the secondary sensory neuron-axons terminates in the lateral cervical nucleus. The efferent fibres of this nucleus also ascend in the contralateral anterior funiculus, as a compact tract, to the inferior olive. From the inferior olive efferent fibres, conveying impulses from all levels of the cord, after crossing, enter the cerebellum via the restiform body.

One point still in need of discussion is the possible segmental arrangement of fibres in the dorsal spinocerebellar tract. This was revealed by Sherrington and Laslett (105) for the first time, and recently it was emphasized by Yoss (128) after an experimental study of the monkey's cord. My experiments, however, did not show any trace of a segmental orientation from dorsomedial to ventrolateral, as was maintained to be the case by Yoss. In the first cervical segment fibres from all levels are thoroughly intermingled. Due to the great addition of fibres at the rostral extremity of Clarke's column, however, fibres originating from this level apply themselves, in a mid-cervical level, medially against the fibres from more caudal origins, already present. In the remaining rostral cervical segments, however, the two fibregroups intermingle, and this intermingling is intensified by the dorsomedial shift of the fibres, present lateral to the rubrospinal tract.

Yoss (128) came to different conclusions, probably either because he studied the monkey or because of the disadvantage that the Marchi technique does not show the normal fibres, present between the degenerated ones.

When Brodal and Rexed (20) described the afferent fibres going to the lateral cervical nucleus they originally were of the opinion that these fibres were situated in the dorsal spinocerebellar tract. When Brodal and Walberg (21) discovered ascending fibres in the pyramidal tract they came to the conclusion that collaterals of these fibres were responsable for the terminal degeneration in the nucleus.

I have not been able to find ascending degeneration in the pyramidal system after spinal cord lesions, not even in longitudinally cut slides. I did find, however, degenerated fibres, coming from the area of the dorsal spinocerebellar tract, which terminated in the lateral cervical nucleus. Terminal degeneration in the nucleus was evident, even in Häggqvist slides. The interpretation of axonal and terminal degeneration in silver-stained slides is very difficult (Glees and Nauta, 44). Possibly even experienced investigators as Brodal and his co-workers may occasionally be misled by the multiform morphology of the axons and their ramifications in their slides.

Another problem is, whether the afferents to the nucleus are really terminating fibres or only collaterals of the dorsal spinocerebellar fibres. I was struck by the number of fibres, contained in the dorsal spinocerebellar tract in a medullary level, being less than at a cervical level caudal to the lateral cervical nucleus. Countings were performed although it is difficult to delineate the dorsal spinocerebellar tract in a cervical level. Nevertheless, the results of these countings show the striking diminution of fibres in the medulla. Moreover, a block of the upper cervical cord, cut longitudinally, in a plane parallel to the fibres entering the lateral cervical nucleus, showed clearly that fibres leave the dorsal spinocerebellar tract, curving from its area in a medioventral direction. Retrograde atrophy of the dorsal spinocerebellar tract after a cerebellar extirpation long before death, leaves many fibres of the tract at C_3 unaltered (H 2720). These fibres, therefore, do not reach the cerebellum and probably are the fibres terminating in the lateral cervical nucleus.

The afferent fibres from the lateral cervical nucleus have al-

ready been described. The physiologically demonstrated dorsal spino-olivary tract (Grundfest and Carter, 50) has now been verified anatomically. These authors found the spino-olivary pathway, composed of thick fibres, to terminate in the contralateral olive after decussation in the uppermost cervical segments. The latency of the impulses arriving at the inferior olive left sufficient time for two synapses of which one was located somewhere in the posterior horn at L_5 where the primary sensory fibres terminate (di Biagio and Grundfest, 9). The lateral cervical nucleus now can be considered to be the second synaps, which they were not yet able to find. The afferent fibres of the lateral cervical nucleus terminate in the caudal and medial parts of the inferior olive.

Wilson and Magoun (125), when demonstrating spino-olivary fibres, severed cervico-olivary fibres only, because they made a cross-section of the cord in the second cervical segment which destroyed the caudal part of the lateral cervical nucleus.

The anterolateral funiculus.

The ascending fibres in the anterolateral funiculus, altogether, were called by Gowers "the anterolateral ascending tract". According to him they represented a crossed pathway for the conduction of pain-impulses. Separate investigations by Singer (106) and Löwenthal (73) demonstrated it as arising in the lower segments of the spinal cord and ascending in the contralateral anterolateral funiculus to a pontine level. There it shifted dorsally to enter the cerebellum via the dorsal surface of the superior cerebellar peduncle. Many disagreements have existed since with regard to its cells of origin. Till 1940 it was accepted that these cells were to be found somewhere in the posterior horn, although they were never clearly demonstrated. Cooper and Sherrington (28) were the first to find retrograde degeneration in the ventral horn of the lumbar cord after hemisection of the anterolateral funiculus cranial to it. They were of the opinion that the so-called ventral "border cells" were the cells of origin of the ventral spino-cerebellar tract. They were not able, however, to demonstrate

cells of the same nature in higher levels, although ventral spinocerebellar fibres arise from higher segments also.

As first proposed by Kohnstamm (60) I call all ascending degeneration in the anterolateral funiculus "the lateral tract of Gowers". The names of Löwenthal and Singer are the ones to be connected with the ventral spinocerebellar fibres, as is Edinger's with regard to the spinothalamic fibres contained in the fascicle. *Functionally the two systems serve completely different functions, morphologically, however, they form an entity.* Fibres only differ in diameter. Later on spinotectal fibres also were described in the fascicle.

Most authors are of the opinion that all ventral spinocerebellar fibres are crossed. My experiments are insufficient to permit a decision. There has not been looked for the cells of origin of the anterolateral ascending fascicle, even though a few experiments gave some evidence of degeneration of border cells as Cooper and Sherrington (28) and Sprague (108, 109) described. Ranson and Clarke, in their textbook, maintain that the ventral spinocerebellar tract mainly conveys impulses from the hind leg, whereas the dorsal tract carries those from the fore leg. This, however, has not been substantiated by my studies. The dorsal spinocerebellar tract receives large numbers of fibres from both ends of Clarke's column, which are in relation to the cervical and lumbar intumescence respectively. The ventral spinocerebellar tract can only be clearly distinguished in the lower part of the thoracic cord. Below this level its fibres are dispersed. They seem to take a long way before gaining their definite position, peripherally in the anterolateral funiculus. This has already been observed grossly by Kohnstamm (60). Nothing in my experiments, however, indicates the presence of a laminar arrangement of fibres from different segments as was described first by Sherrington and Laslett (105) and recently by Yoss (129) in the monkey. These authors indicate that caudal fibres lie dorsolateral in the tract and rostral fibres ventromedial to them. From my experiments I got the impression that fibres from all levels are thoroughly intermingled. Only when large numbers of fibres

join the fascicles, as happens in the cervical intumescence, the new fibres apply themselves centrally against those already present. One or two segments more rostrally, however, concentric lamellas are no longer seen, the new fibres having intermingled with the others, already present. Marchi slides show only the degenerated fibres and, therefore, may give the illusion of a segmental localization in the fascicle. Häggqvist's technique, however, shows normal fibres between the degenerated ones and consequently does not confirm this.

Ever since Edinger (30) discovered spinothalamic fibres, much attention has been paid to this system. Soon after the discovery of the spinothalamic fibres, their presence in the anterolateral funiculus was denied by Mot (86), Schäfer (103) and others. Most of the positive reports about these fibres are based upon human material or experiments on monkeys. The presence of direct spinothalamic fibres in the cat has never been conclusively demonstrated anatomically.

In this century the spinothalamic system became very important because of the surgery of pain and most of the additional information about this system is based on the results of anterolateral chordotomies, performed in man. In recent years many investigators have been upset by the fact that so few fibres enter the thalamus in comparison with the large amount of degeneration present in the anterolateral funiculus of the cord, rostral to a transverse lesion (Gardner and Cuneo (35), White (124), Walker (120, 121), Rasmussen and Peyton (97) a.o.).

Recent experiments on monkeys confirm this observation in man. Glees (42) found not more than 1500 fibres in the mesencephalon, entering the thalamus after a spinal lesion. In the monkey these fibres were even much less and in the cat he was not able to find any. Morin et al. (82, 84 en 85) had the same results and they were of the opinion that most ascending fibres, conveying impulses to the thalamus, were interrupted in the reticular formation of the medulla.

Neurosurgical results led many authors to accept a topical arrangement of the fibres in the spinothalamic system. How-

ever, it appeared to be different with each author. Foerster and Gagel (33) found that caudal fibres lay peripherally and proximal fibres centrally, in concentric lamellas, fibres filling the whole anterolateral and anterior funiculus. The fibres for temperature perception lay dorsally, those for touch ventromedially and those for pain in between. Hyndman and Van Epps (55) found the fibres from the leg to lie most dorsally and those from the chest most ventromedially. This arrangement is also accepted by Riley (100). Walker (120) found parallel lamellas of fibres in which the sacral fibres were situated dorsolaterally and the cervical fibres ventromedially. They filled the complete anterolateral funiculus.

In the recent study of Yoss (129, 130) on monkeys, the spinothalamic fibres were situated central to the ventral spinocerebellar ones, showing the same lamination as was accepted by Walker in man. From my experiments on the cat, however, this is not confirmed, since the thinner ascending fibres, not going to the cerebellum, lie partially among the spinocerebellar fibres and partially medial and ventral to them, scattered between other fibres of the anterolateral funiculus. They cause the medial border of the anterolateral fascicle of Gowers to be very vague. Kennard (59) recently maintained that spinothalamic fibres in the cat are found in the posterolateral funiculus of the cord and dorsal to the inferior olive in the medulla. She was not able to demonstrate them anatomically and the existence of such ascending fibres, in appreciable numbers in the posterolateral funiculus, could not be confirmed from my slides.

One of the striking facts, established by this study, is that degeneration in the anterolateral funiculus above a hemichordotomy is very large, whereas the corresponding degeneration in a medullary level is very sparse. Only a few thick fibres can be followed into the cerebellum, via the superior cerebellar peduncle. All the other ones are lost when the anterolateral ascending fascicle of Gowers is dispersed at the level of the lateral reticular nucleus. Single fibres and small groups of degenerated fibres are present everywhere in this nucleus, most

of them terminating in it. *Not one fibre, present rostral to the lateral reticular nucleus, can be followed into the optic tectum and the posteroventral nucleus of the thalamus.*

The same results were obtained by Morin, Schwartz and O'Leary (85) who also were of the opinion that most of the ascending fibres were interrupted in the reticular formation of the medulla. They, however, found degeneration of fibres, belonging to the spinothalamic system, dorsal to the inferior olive. This I was not able to confirm. Glees (42, 43) could find some spinothalamic fibres in the monkey, but not one was present in the mesencephalic tegmentum of the cat. *Evidence is accumulating therefore, that in lower mammals such as the cat, all spinothalamic connections are interrupted in the reticular formation of the medulla.*

My experiments showed that the fibres of Gowers' fascicle terminate to a large extent in the lateral reticular nucleus. Brodal (18, 19) found that this nucleus sends its efferent fibres to the homolateral cerebellum. This I can agree with, since nearly all cells of the nucleus degenerate and disappear in chronic cerebellar ablation cases. This nucleus, therefore, can not be other than a relay in a spinocerebellar connection.

According to Brodal (19) somatotopic localisation is rather poor in the nucleus. This is not astonishing for I was not able to find any topical organization in the afferent tract. The afferents to the lateral reticular nucleus have already been investigated to some extent by Blakeslee, Freiman and Barrera (11) and my results are in accordance with theirs. If this nucleus is a spinocerebellar relay nucleus, however, it is difficult to imagine how the spinothalamic system should be interrupted in this nucleus. A possible passage of spinothalamic impulses via the cerebellum and the red nucleus can be rejected: the latency with which impulses reach the thalamus from a peripheral source would be much longer in this case than it is in reality (Morin, 82).

Close inspection of the medulla, however, reveals that the most medial fibres of the ascending fascicle of Gowers do not terminate in the lateral reticular nucleus but terminate around

small reticular cells situated more medially, just lateral to the medial lemniscus. Rostral to the lateral reticular nucleus, upwards to the trapezoid body level, such termination of thin fibres around scattered reticular cells is evident. These cells, situated in a lateroventral part of the reticular formation, do not belong to a specific reticular nucleus. It can be imagined that the axons of these cells are directed towards the thalamus. It will be clear that it is difficult to destroy these rather diffuse cells in sufficient numbers to obtain an appreciable thalamopetal fibre degeneration, though the experiment seems worth to be endeavoured.

Edinger (30) and Auerbach (4) a.o. were of the opinion that pain-conveying fibres were present in the anterolateral funiculus. Recent experiments by Kennard (59) showed that the dorsolateral funiculus was essential to pain transmission in the cat. Unfortunately, our material does not contain sections of the anterolateral funiculus alone. I was not able, however, to find any structure in the posterolateral funiculus which could be held responsable for pain conduction, except for a small number of stray fibres. Her argument that a small or absent lateral pyramidal tract might be the cause of this dorsal position of the spinothalamic fibres does not hold, since the cat has a well-developed lateral pyramidal tract which fills half of the posterolateral funiculus. Nevertheless, the possibility must be taken into account that spinothalamic fibres in the cat have their site outside the anterolateral funiculus.

Physiologic experiments by several investigators point to the possibility that there should be an interruption of the spinothalamic tract in the reticular substance. I will not go deeply into this point because it is beyond the scope of this thesis. Reference can be made to Mountcastle and Henneman, Berry, Karl and Hinsey (8) and recently Morin (82).

If we review the ascending fibres of the anterolateral funiculus we see that it consists of spincerebellar fibres and two or possibly more kinds of spinoreticular fibres, viz: a spinoreticulo-cerebellar pathway, a spino-reticulo-thalamic and a spinoreticulo-tectal pathway.

As stated above many investigators saw only a minority of ascending fibres from the anterolateral funiculus enter the thalamus. The number of these fibres is supposed to be larger in man than in the monkey. It might be hypothesized that the number of direct spinothalamic fibres increases through the phylogenic scale from zero in the cat to some thousands in man. The remaining fibres from the cord to the thalamus can be assumed to be interrupted in man, as is the case with all of them in the cat.

THE DESCENDING FIBRESYSTEMS.

The pyramidal tract.

The pyramidal tract is one of the most investigated tracts of the central nervous system and the experiments performed in this study can not be expected to yield much additional information. Since von Monakow (80) pointed out that the pyramidal tract arises from a larger cortical area than the motor cortex alone, many investigations have been performed with the intention to specify the exact origin of fibres of the pyramidal tract outside the motor cortex.

McKibben and Wheelis (76) located the motor cortex of the cat in the anterior and posterior sigmoid gyrus, but more recent investigations have pointed out that the posterior sigmoid gyrus must be regarded as part of the sensory cortex. Antidromic stimulation of the pyramidal tract of the cat by Woolsey and Chang (127), apart from both sigmoid gyri and surrounding cortex, also activated the second somatic area. Recently, Walberg and Brodal (118) found that fibres from the temporal and occipital lobes of the cat descend in both lateral as well as both ventral pyramidal tracts. Their results were preceded by those of Gobbel and Liles (45) who found fibres from the parietal lobe of the cat, descending only in the lateral pyramidal tract and not beyond the cervical cord. They, however, used the Marchi technique which is inferior to the silver technique.

My experiments also gave me the impression that many fibres of the pyramidal tract arise outside the motor cortex in the cat,

but that no fibres are added from a subcortical level above the decussation. The percentage of these extramotor pyramidal fibres does not exceed 20 % of the total amount of fibres, contained in the medullary pyramid. The number of pyramidal fibres in a cervical level, affected after a motor ablation, does not exceed half of the fibres present in the medullary pyramid. This means that many fibres terminate at the transition of the medulla and the cord, because the total number of pyramidal fibres has also decreased.

The number of normal fibres in the lateral pyramidal tract of the cord is still considerable after a complete cortical ablation, which destroys almost all of the fibres in the medullary pyramid.

Lassek in 1946 (65), with motor cortex ablations, found that the number of normal fibres in the spinal lateral pyramidal tract was much larger than in the medullary pyramid. This can not be attributed to uncrossed fibres joining the lateral pyramidal tract, since these fibres are much too rare to account for this large difference between the pyramid and the cervical lateral pyramidal tract. Moreover, Lassek found that an additional ipsilateral motor cortex ablation did not change the aspect of the cervical lateral pyramidal tract appreciably. Therefore it is justified to conclude that many of the fibres within the cervical lateral pyramidal tract originate at the level of transition of the medulla and the cord. My experiments confirm this cimpletely. After a survey of the literature Nathan and Smith (88) admit that the presence of foreign fibres in the lateral pyramidal tract in the cord is probable, but they point out that it is very difficult to compare different specimens with each other. Rubrospinal and propriospinal fibres may be the cause of the phenomenon that the lateral pyramidal tract often is different in different specimens. The analysis of fibres with Häggqvist's method, however, allows precise differentiation of rubrospinal and pyramidal fibres. Therefore, it seems to me that the statement that also fibres from the reticular formation descend in the lateral pyramidal tract, is correct. Farther downwards descending propriospinal fibres enter the lateral pyramidal tract. No ascending fibres were observed in this area.

A problem to be discussed, together with that of the additional fibres in the spinal pyramidal tract, is the length over which this tract descends in the cord. Lassek (65) could follow its fibres to the first lumbar segment, McKibben and Wheelis (76) traced them down to the lower sacral cord. In the monkey the fibres, in most of the cases, have been followed into the sacral segments. Brookhart and Morris (14) were able to activate the medullary pyramid in the cat by stimulation of the cord as far down as the sixth lumbar segment. Lance (62) however, could not pick up responses in the area of the lateral pyramidal tract below the fourth lumbar segment when stimulating the medullary pyramid. In the present experiments, after decortication, degeneration was noted down to the fifth lumbar segment. It, however, extended farther downward after severance of the pyramidal tract in the cord, the farther was the degeneration the lower the section was carried out. Therefore it can be considered as certain that *the lateral pyramidal tract area carries relatively large numbers of fibres arising at different levels of the cord and descending over some distance in it.* Many of these fibres descend farther than the corticospinal fibres and it is conceivable to reflect on the possibility that the former fibres have something in common with the latter ones.

Hoff (53) and also Lloyd (70) came to the conclusion that the pyramidal fibres do not end on the anterior horn motor neurons but on intercalate neurons in the intermediate part of the spinal grey matter. This implies that there is a secondary motor neuron carrying the cortical impulses to the motor neuron. In accordance with this there may be another secondary motor neuron which does not connect the pyramidal fibre with the motor neurons in the level of the former's termination but a number of segments more caudally. The axons of such neurons can be supposed to have a tendency to join the lateral pyramidal tract or its area, and it seems not too far fetched to suggest that the additional spinal fibres of the lateral pyramidal tract chiefly consist of such axons. Lassek (65) considered the existence of secondary pyramidal neurons in the cord of animals

with a rudimentary spinal pyramidal tract, that does not descend beyond the uppermost cervical segments. The opinion is generally held that in "lower" mammals the spinal pyramidal tract is rudimentary and especially in such animals the secondary neurons may be of importance. According to Lassek the cat is intermediate between those "lower" mammals and the primates in which corticospinal fibres of great length are abundant.

In this study it has been conclusively demonstrated that many pyramidal fibres terminate at the level of transition of the medulla and the cord and that on the other hand many additional pyramidal fibres originate at about the same level. Presumably the same is the case at most levels of the cord where real pyramidal fibres are still to be found. Quantitative relations between terminating and originating fibres at a certain level, however, are still entirely unknown. The only thing to be stated is, that a considerable overlapping of primary and secondary pyramidal neurons exists since at a level where decortication causes a pronounced degeneration, this degeneration is conspicuously increased by an additional ipsilateral chordotomy, rostral to that level. This is not at all astonishing, since it is established that the corticofugal fibres terminate at different levels and in the scope of the hypothesis it may be assumed that, accordingly, also secondary pyramidal fibres arise at many levels.

As to the question whether or not in the cat an uncrossed ventral pyramidal tract is found opinions, reported in literature, differ considerably. Lassek (65) maintains that no such tract exists and Lance (62), using physiologic experiments, came to the same conclusion. Brodal and Walberg (118) on the contrary, after a unilateral motor cortex ablation, found degeneration in both lateral as well as both ventral pyramidal tracts. In none of the present experiments a trace of a ventral pyramidal tract was noticed, and uncrossed fibres within the lateral tract proved to be very rare. This discrepancy is only comprehensible when the ventral tract consists only of unmyelinated fibres which do not show in Häggqvist-stained slides, but this seems unprobable.

Ascending fibres within the pyramidal tracts, as reported by

Brodal and Walberg (21), were not noticed in any of the numerous chordotomy cats. The authors state that these fibres give off collaterals to the lateral cervical nucleus, but it was proved that the latter nucleus gets its afferents from the dorsal spinocerebellar tract area.

The rubrospinal tract.

The location of the rubrospinal tract in the cord of the cat has already been pictured by Gray (46) in his study on the vestibular mechanism, and van Gehuchten (37), in the beginning of this century, pointed to the close relationship between the rubrospinal and the ventral spinocerebellar fibres. Mettler (77) indicated the tract in the monkey and found that it descended to the sacral segments. The present results are in complete accordance with theirs and not much additional information can be offered. Publications dealing with the fibre composition of the tract are rare. Verhaart (115) stated that the tract in the cord is composed of thick rubrospinal fibres, together with many thin fibres of a different origin. My experiences show that in the cat the rubrospinal fibres are scattered over a large area and that they by no means form a homogeneous tract, which until now had been most generally assumed. Only Mettler (77) pointed to the fact that rubrospinal fibres lie scattered in the lateral part of the pyramidal area. This he could confirm over the complete length of the cord. Everywhere where rubrospinal fibres occur they are a numerical minority, but they show conspicuously because of their large diameter. In their area pyramidal, spinocerebellar, reticulospinal and propriospinal fibres also are found.

The medial longitudinal fascicle.

The medial longitudinal fascicle is a very composite system which contains fibres of many origins. Most investigations deal with the fibres of vestibular origin only. A survey of the literature shows that there is not too much agreement about the position of the fibres from the different vestibular nuclei in it. This is probably due to the difficulty in severing the

different parts of the vestibular complex selectively. As some authors remark the reticular substance is often severed along with the vestibular nuclei, with subsequent degeneration of reticulospinal fibres in the fascicle which can be mistaken for vestibulospinal ones. The lesions which I made in the vestibular complex were not sufficiently selective to make positive statements and the results I described are only approximations which I got from comparing the different experimental specimens with the normal aspect and fibre structure.

The fibres from the superior vestibular nucleus terminate in the medulla and do not descend into the cord. Some fibres from the lateral nucleus are present in the centre of the homolateral fascicle. Fibres from the medial and descending nucleus are present bilaterally. Those from the descending nucleus are situated most dorsally. Part of these vestibulospinal fibres in the fascicle can be followed to the most caudal segments of the cord, where they retain their position in the medial part of the anterior funiculus. These results are in complete accordance with those obtained by Rasmussen (95) but differ from those of other investigators.

More positive statements were reported on the location of the interstitiospinal and tectospinal fibres contained in the fascicle. The interstitiospinal fibres in the pons are situated very dorsally, but in the medulla they are pushed ventrally by the addition of new fibres which enter the fascicle dorsally. In the cord the fibres again are situated very dorsally because the fibres, dorsal to them in the medulla, have shifted ventrally. The interstitiospinal fibres can not be followed below the 7th cervical segment.

The tectospinal fibres of the fascicle all arise in the contralateral superior colliculus, and initially are situated in the predorsal fascicle. In the medulla, when this fascicle fuses with the medial longitudinal fascicle, they lie in the ventral part of the medial longitudinal fascicle. These fibres can be followed into the highest thoracic segments. Rasmussen (96) reported analogous results.

Reticulospinal fibres enter the medial longitudinal fascicle in the medulla to such an extent that it becomes nearly twice as

large. They are of two kinds: first there are thick ones, closely resembling the vestibulospinal fibres, which enter it in a high medullary level and second, there are thin fibres that enter it somewhat more caudally from laterally. The latter change its fibrespectrum completely, since above this level most fibres are thick and medium-sized, but now many thin fibres are present between the thicker ones. At the lowermost part of the medulla again many thick fibres arise which partly apply themselves to the lateroventral part of the fascicle. The firstmentioned group presumably represents P a p e z' medial reticulospinal tract and the lastmentioned group, which for the larger part lies between the medial longitudinal fascicle and the vestibulospinal tract, his ventral reticulospinal tract (90). It should be emphasized that the fibres are too scattered to be called a tract. Moreover, many of them are found in other parts of the anterior and lateral funiculi of the cord.

The thick reticulospinal fibres can be followed in the cord to the lower parts of the cervical and the highest segments of the thoracic cord, whereas the thin ones seem to terminate more rostrally.

In the cord many thick propriospinal fibres, which look exactly like the fibres already present, are added to the fascicle. They cause the fascicle to look larger than it would be if only supraspinal fibres were contained in it. Possibly these thick propriospinal fibres relay impulses conveyed by fibres which already in the brain stem belong to the medial longitudinal fascicle.

The vestibulospinal tract.

It is generally accepted that the vestibulospinal tract originates from the lateral vestibular nucleus of the same side. This could be substantiated in the present study. Only thick fibres, however, have there origin in the nucleus of D e i t e r s, whereas besides such fibres many thin ones are contained in the tract in a high spinal level. These thin fibres come from the reticular substance of the medulla and descend together with those of the lateral vestibular nucleus. A fibrespectrum of the tract,

therefore, is of no value. The fibres of the tract descend to the lowest levels of the cord but lose their separate position. They are scattered peripherally in the lateral part of the anterior and in the anterolateral funiculus. No new facts have been added to those already known about this system.

Remaining fibres in the anterolateral white matter.

The posterolateral funiculus is almost completely filled with long ascending and descending systems. Only a small strand of white matter with very thin fibres is present between the posterior horn and the lateral pyramidal tract. These fibres probably are short associative neurites which connect successive levels of the posterior horn. In this respect they may be considered to be part of the fasciculus proprius.

The anterolateral funiculus contains a large area not occupied by circumscribed fibresystems. In this area, Häggqvist's area 7, the fibres are mostly of small calibre. The lower the level the fewer are the fibres identifiable. At a short distance from a hemichordotomy it contains many normal fibres again and even between a double hemichordotomy a relatively large amount of normal fibres is preserved in it. It can be distinguished from the fasciculus proprius, around the ventral horn, by its higher contingent of thick fibres. The fibres of the long ascending systems, originating contralaterally, pass through this area. Diffuse systems have been described in it, most of them belonging to the sympathetic nervous system.

In the lower part of the cord this area extends into the ventral and medial part of the posterolateral funiculus, and besides this occupies the larger part of the anterior funiculus. It is remarkable that even at a short distance from the lesion in an isolated portion of the cord, so many normal fibres are present in all known systems, and predominantly in those parts where no systems occur. The only area which seems to remain free of these short fibres is the dorsal spinocerebellar tract.

The bulk of the white matter in the lower part of the cord

exists of propriospinal neurites, part of these relaying impulses of supraspinal systems to lower levels.

Tower, Bodian and Howe (114) examined the intrinsic mechanism of the spinal cord. Their anatomical results are largely identical to those presented here. According to Lloyd (70, 71) many of these fibres are intercalated neuron axons that relay supraspinal impulses. As stated, my experiments gave me the impression that many systems which descend into the cord exert their influence over a much larger part of the cord than would be expected from the length of their fibres.

In the same way ascending systems seem to consist partially of fibres which are interrupted during their ascent in the cord. The meaning of this is not at all clear, but it can be hypothesized that it leads to some sort of integration of different impulses and of different systems.

SUMMARY.

The spinal cord of the cat has been investigated, and special attention has been paid to the anterior and lateral white matter. The study has been performed largely with Häggqvist's technique which allows an analysis of the normal aspect of the known fibretracts. Additional information was obtained from experiments, and the resulting degeneration was studied with the same technique which shows the degeneration conspicuously.

The result was that most fibresystems can be better recognized by their aspect in the Häggqvist slide than by a spectrum, to be established by counting and measuring the constituent fibres.

It was found that the dorsal spinocerebellar tract arises largely from both extremities of the homolateral column of Clarke. Many fibres, however, are present in its area which offered the same aspect but differed from the spinocerebellar ones by their more caudal origin and by their termination. Part of these fibres terminate in the posterior horn in higher levels and part of them terminate in the lateral cervical nucleus, which efferent fibres cross and terminate in the inferior olive. In this way *a spino-cervico-olivo-cerebellar pathway* was found to exist in the posterolateral funiculus, which receives its fibres from all levels of the cord. Many of the fibres contained in the dorsal spinocerebellar tract proved to be propriospinal ones.

The ventral spinocerebellar tract appeared to be built up of fibres originating from all levels of the cord, probably arising at the contralateral side from ventral border cells. Part of its fibres appeared to terminate in the lateral reticular nucleus, and so a *spino-reticulo-cerebellar-pathway* has been established in the anterolateral funiculus of the cord.

No spinothalamic fibres could be found in the central nervous system of the cat, and the same holds for the spinotectal fibres.

All ascending fibres of the anterolateral funiculus, except the ventral spinocerebellar ones, terminate in the lateral reticular nucleus or in the ventrolateral reticular substance of the medulla. It has been assumed that from this region *secondary fibres travel to the thalamus and the optic tectum.*

A systematic localization of fibres from different segments could not be found, neither in the dorsal nor in the ventral spinocerebellar tract. New fibres apply themselves to the centrally directed border of the tract and, soon afterwards, are taken up into the area of the tract without clustering together.

Very few spino-olivary fibres could be found which reach the inferior olive together with the cervico-olivary fibres. The spino-olivary fibres are located along the periphery of the anterior funiculus.

No ventral pyramidal tract could be located in the cord of the cat. Only a very small number of pyramidal fibres go to the lateral tract of the same side. Many pyramidal fibres appeared to terminate in the reticular formation of the transition of medulla and spinal cord. This reticular formation is found mainly at the base of the posterior horn. Some fibres were seen to terminate in the anterior horn. Many new fibres arise in this region and join the lateral pyramidal tract. During the descent of the pyramidal fibres in the cord they terminate at all levels, but mostly at the enlargements. Many new thin fibres are added to the lateral pyramidal tract but not in sufficient numbers to replace the ended fibres. From comparisons between the degeneration of the lateral pyramidal tract after a cortical ablation and after a cord lesion, it appeared that fibres of spinal origin, contained in the tract, descend farther downwards than the corticospinal fibres. It has been supposed that these fibres belong to relay neurons, which extend the cortical influence farther down into the cord than indicated by the length of the corticospinal fibres. The corticalspinal fibres do not descend below L 5, whereas the spinal relay fibres descend to the lowermost segments.

The rubrospinal tract appeared to be composed of thick fibres only, scattered over a large area in the lateral funiculus.

Many thin fibres descend with them from brain stem levels into the cord, but these have a different origin. Rubrospinal fibres intermingle to a large extent with the lateral pyramidal and the ventral spinocerebellar fibres. They descend into the lower sacral segments.

The medial longitudinal fascicle appeared to be very composite and the intermingling of fibres from different sources seemed to be its chief characteristic. It contains many thick fibres, whereas thin fibres enter the fascicle chiefly in low medullary levels.

These thin fibres are mainly reticulospinal ones. The bulk of the fascicle is composed of vestibulospinal fibres, from the medial and descending nucleus mainly. Besides these, interstitional fibres descend in the medial longitudinal fascicle to the 7th cervical segment and tectospinal fibres to the second thoracic segment. In the spinal cord thick propriospinal fibres join the fascicle and, therefore, it appears larger than if only the supraspinal fibres, contained in it, are considered. These supraspinal fibres are the ones which from all supraspinal fibres descend farthest in the cord.

The vestibulospinal fibres of Deiters are the thick ones, contained in an area in the anterior funiculus, which contains also other fibres. Most of the fibres terminate in the cervical enlargement, but some can be followed to the lumbar enlargement. In the thoracolumbar segments it is impossible to speak of a vestibulospinal tract. The vestibulospinal fibres are scattered widely apart, completely peripherally along the pia mater of the anterior and anterolateral funiculus.

No more or less circumscribed reticulospinal pathways could be localized. Reticulospinal fibres are present everywhere in the anterior and anterolateral funiculus. Most of them are contained in the descending tracts as the rubrospinal, the vestibulospinal and especially the medial longitudinal fascicle. Scattered reticulospinal fibres are present around the ventral horn, but they do not descend far into the cord.

The fasciculus proprius is composed of thin and short ascending and descending fibres in equal numbers, not exceeding two

segments in length. Otherwise, propriospinal fibres occur everywhere, even in presumably homogeneous tracts, such as the dorsal spinocerebellar tract.

In conclusion it may be stated that no pure tracts occur in the cord of the cat, neighbouring systems intermingling to a considerable extent. We will have to abandon the idea of a tract as a bundle of fibres of the same nature. A tract could be better defined *as an area of white matter with a specific fibre-pattern, in which fibres of a certain nature predominante.* In the case of the medial longitudinal fascicle this definition is even not correct. Often it will be more appropriate to speak of a fibresystem instead of a tract.

RESUME.

Dans cette étude sur la moëlle épinière du chat l'attention a été spécialement fixée sur la matière blanche du funicule antérieur et latéral. L'étude a été établie à l'aide de la méthode d'Häggqvist, qui permet l'analyse des fibres constituant les faisceaux connus.

Information additionelle fut obtenue à la suite d'expériences et la dégénération axonale consécutive put être observée nettement dans la coloration d'Häggqvist en relation avec les fibres normales.

Le résultat montra que la plupart des systèmes fibreux sont mieux reconnus par leur aspect, ainsi que le montre la coloration d'Häggqvist, que par leur spectre fibreux, établi en mesurant et comptant les fibres.

Il fut démontré que le faisceau spinocérébelleux dorsal a son origine en grande partie dans les deux extrémités de la colonne de Clarke homolatérale. Beaucoup de fibres contenues dans le champ spinocérébelleux dorsal ont une terminaison différente et une origine plus caudale que les fibres spinocérébelleuses, bien qu'elles aient le même aspect. Une partie de ces fibres se termine dans la corne postérieure, quelques segments plus haut et l'autre partie se termine dans le noyau cervical latéral. Les fibres efférentes de ce noyau s'entrecroisent et se terminent dans l'olive inférieure. De cette façon une *connection spino-cervico-olivo-cérébelleuse* fut trouvée dans le funicule postérolatéral qui reçoit ses fibres de tous les segments de la moëlle épinière. Beaucoup de fibres du faisceau spinocérébelleux dorsal ont paru être des fibres propriospinales.

Le faisceau spinocérébelleux ventral parut être composé de fibres de tous les segments de la moëlle épinière, qui ont probablement leur origine dans les cellules antérieures latérales du côté op-

posé. Une partie des fibres du champ spinocérébelleux ventral se termine dans le noyau réticulaire latéral et ainsi la présence d'un *système spino-réticulo-cérébelleux* fut démontré dans le funicule antérolatéral.

Aucune fibre spinothalamique et spinotectale fut trouvée dans le système nerveux central du chat. Toutes les fibres ascendantes du funicule antérolatéral, sauf celles du faisceau spinocérébelleux ventral, se terminent dans le noyau réticulaire latéral de la moëlle oblongée ou bien dans la partie ventrolatérale de la substance réticulaire. Il fut supposé que de cette partie *des fibres secondaires se dirigent vers le thalamus et la couche optique du mésencéphale.* Ces fibres sont probablement très diffuses, ce qui explique pourquoi elles ne furent pas encore localisées. La connection spinothalamique chez le chat est probablement interrompue une ou plusieurs fois dans le tronc cérébral.

Une localisation systématique des fibres des différents segments ne put être trouvée dans le faisceau spinocérébelleux dorsal ni dans le faisceau ventral. De nouvelles fibres s'accollent médialement au faisceau auquel elles appartiennent et peu après se dispersent dans ce système. Peu de fibres spino-olivaires, atteignant l'olive inférieure avec les fibres cervico-olivaires, furent trouvées. Ces fibres spino-olivaires sont situées le long de la périphérie du funicule antérieur.

Il fut impossible de trouver un faisceau pyramidal non-croisé dans le funicule antérieur chez le chat. Il n'y a qu'un très petit nombre de fibres pyramidales non-croisées dans le faisceau latéral. Beaucoup de fibres pyramidales se terminent après s'être croisées dans la formation réticulaire à la transition de la moëlle oblongée et la moëlle épinière. Cette formation réticulaire est située principalement à la base de la corne postérieure. On put néanmoins observer quelques fibres se terminant dans la corne antérieure. Beaucoup de nouvelles fibres ont leur origine dans cette région de la formation réticulaire et se joignent au faisceau pyramidal latéral.

Les fibres pyramidales se terminent dans tous les segments de la moëlle épinière mais surtout dans les intumescences.

Beaucoup de nouvelles fibres s'ajoutent au faisceau pyramidal latéral, mais pas en nombre suffisant pour remplacer les fibres terminées. Ces fibres spinales causent, à la suite d'une lésion spinale, une dégénération pyramidale plus forte qu'à la suite d'une lésion corticale. Il fut aussi nettement visible que ces fibres propriospinales, contenues dans le faisceau pyramidal latéral, descendent plus bas dans la moëlle épinière que les fibres pyramidales elles-mêmes. Il fut supposé que ces fibres relaient des impulsions pyramidales et qu'ainsi l'influence pyramidale s'étend sur un rayon plus grand que l'on aurait pu préconiser, vu la longueur des fibres pyramidales. Les fibres corticospinales ne descendent pas plus bas que le cinquième segment lombaire, tandis que les fibres propriospinales peuvent être suivies jusque dans les segments les plus bas.

Le faisceau rubrospinal est composé uniquement de fibres épaisses, dispersées sur une grande surface triangulaire dans le funicule latéral. Beaucoup de fibres plus minces descendent avec elles du niveau du tronc cérébral dans la moëlle, mais celles-ci ont une origine différente. Les fibres rubrospinales s'entremêlent considérablement aux fibres pyramidales latérales et aux fibres spinocérébelleuses ventrales. Elles descendent jusque dans les segments sacraux les plus bas.

Le faisceau longitudinal médial sembla être un système très complexe, dont l'entremêlement des fibres de différentes origine fut la caractéristique principale. Il contient beaucoup de fibres épaisses, tandis que les fibres minces entrent en grande partie dans le faisceau à un bas niveau de la moëlle oblongée. Ces dernières sont principalement des fibres réticulospinales. La plupart des fibres du faisceau longitudinal médial ont leur origine dans les noyaux vestibulaires et surtout du médian et du descendant. A part celles-ci, des fibres interstitiospinales descendent dans le faisceau jusqu'au 7ième segment cervical, et des fibres tectospinales jusqu'au second segment thoracique. Dans la moëlle épinière d'épaisses fibres propriospinales entrent dans le faisceau longitudinal, c'est pourquoi il paraît plus grand que si l'on ne considérerait uniquement les fibres supraspinales contenues en lui. Ces fibres supraspinales, comparées aux fibres

supraspinales d'autres systèmes sont les plus longues de la moëlle épinière.

Les grosses fibres vestibulospinales sont situées dans une aire du funicule antérieur qui contient également d'autres fibres plus minces de la moëlle oblongée. La plupart des fibres vestibulospinales se termine dans l'élargissement cervical, mais certaines peuvent être suivies jusqu'à l'élargissement lombaire. Il est impossible de parler d'un faisceau vestibulospinal dans les segments thoracolombaires, parce que ces fibres sont fort dispersées le long de la périphérie du funicule antérieur et antérolatéral.

Il fut impossible de localiser des faisceaux réticulospinaux bien limités. Des fibres réticulospinales sont présentes partout dans le funicule antérieur et antérolatéral. La plupart de celles-ci sont contenues dans les faisceaux descendants tels que le faisceau rubrospinal, vestibulospinal et spécialement le faisceau longitudinal médial. Des fibres réticulospinales dispersées furent trouvées autour de la corne antérieure, mais celles-ci ne descendent pas loin dans la moëlle épinière.

Le faisceau cornumarginal est composé de fines et courtes fibres ascendantes et descendantes, elles ne sont pas plus longues que deux segments au maximum. D'ailleurs des fibres propriospinales sont présentes dans tous les systèmes de la moëlle, même dans les systèmes considérés comme homogène des fibres pareilles mais plus longues sont présentes.

Nous pouvons conclure qu'il n'y a aucun système pure dans la moëlle épinière du chat et que les systèmes voisinants entremêlent leurs fibres considèrablement. Nous devons donc abandonner l'idée qu'un faisceau est composé de fibres de même nature. Une meilleure définition d'un faisceau serait: *Une aire de matière blanche avec un spectre fibreux spécifique dans lequel les fibres d'une nature prédominent.* Néanmoins cette définition n'est pas tout à fait correcte pour le faisceau longitudinal médial. Souvent il vaudrait mieux employer le terme système fibreux au lieu de faisceau.

SAMENVATTING.

In deze studie van het ruggemerg van de kat is de aandacht speciaal gevestigd op de vezelsamenstelling van de funiculi anterior en lateralis. De studie is voor het grootste deel gebaseerd op materiaal dat werd gekleurd volgens de Häggqvist modificatie van de Alzheimer-Mann glia kleuring met methylblauw en eosine. Deze methode maakt een analyse mogelijk van het normale aspect der bekende vezelsystemen.

Door experimenten werden aanvullende inlichtingen verkregen omtrent de vezelsamenstelling van de voorzijstreng. Degeneratie van vezels is met de Häggqvist methode uitstekend waar te nemen, terwijl hun relatie tot normale vezels zichtbaar is.

Het bleek al spoedig dat de meeste vezelsystemen beter herkend kunnen worden aan hun aspect in de Häggqvist coupes dan aan hun vezelspectrum, door tellen en meten vastgesteld.

Het bleek dat de dorsale spinocerebellaire baan voor het grootste deel ontspringt van de beide uiteinden van de homolaterale zuil van Clarke. Veel vezels, welke in de baan voorkwamen en er net eender uitzagen als de spinocerebellaire, bleken een totaal verschillende eindiging te bezitten en hun oorsprong lag voor een deel ook veel verder caudaal. Een deel van deze vezels eindigt in de achterhoorn, enkele segmenten hoger en een ander deel eindigt in de nucleus cervicalis lateralis. De efferente vezels van deze kern kruisen en eindigen in de oliva inferior. Op deze wijze werd een *spino-cervico-olivo-cerebellair systeem* gevonden in de funiculus posterolateralis, welk zijn vezels ontvangt uit alle ruggemergssegmenten. Veel vezels in de dorsale spinocerebellaire baan bleken propriospinale vezels te zijn.

De ventrale spinocerebellaire baan bleek te zijn opgebouwd uit vezels uit alle segmenten van het ruggemerg, welke waarschijnlijk

hun oorsprong hebben uit laterale voorhoorncellen, contralateraal. Een deel van de vezels, liggende in het ventrale spinocerebellaire areaal, bleek te eindigen in de nucleus reticularis lateralis en dus bleek er een *spino-reticulo-cerebellair systeem* te bestaan in de funiculus anterolateralis.

Er werden geen spinothalamische, noch spinotectale vezels gevonden in de funiculus anterolateralis bij de kat. Alle opstijgende vezels in dit gebied, behalve de ventrale spinocerebellaire, eindigen of in de nucleus reticularis lateralis van het verlengde merg of in de ventrolaterale reticulaire substantie, mediaal en rostraal van de nucleus reticularis lateralis. De mogelijkheid is geopperd dat van dit gebied uit reticulothalamische en reticulotectale vezels opstijgen, waarschijnlijk zeer diffuus, en *aldus zou de spinothalamische verbinding bij de kat een of meer malen onderbroken zijn.*

Noch in de dorsale, noch in de ventrale spinocerebellaire baan kon een systematische rangschikking van vezels uit de verschillende segmenten worden aangetoond. Juist ontstane vezels leggen zich mediaal tegen de baan waarbij ze behoren en worden dan spoedig in dit systeem opgenomen, waarbij ze niet bij elkaar blijven liggen om op deze wijze een topographische laminering te doen ontstaan.

Slechts enkele spino-olivaire vezels konden worden gevonden, welke de oliva inferior bereiken samen met de cervico-olivaire vezels. Deze spino-olivaire vezels liggen langs de peripherie van de funiculus anterior.

In het ruggemerg van de kat was het niet mogelijk een ongekruiste ventrale pyramidebaan aan te tonen in de funiculus anterior. Slechts een klein aantal vezels kruist niet en komt in de homolaterale pyramidebaan terecht. Veel pyramidevezels bleken te eindigen na hun kruising in de reticulaire formatie, op de grens van medulla oblongata en ruggemerg. Deze reticulaire formatie is hoofdzakelijk aan de basis van de achterhoorn gelegen. Tenslotte werd waargenomen dat enkele vezels na hun kruising eindigden in de voorhoorn. In dit gebied van reticulaire stof ontstaan ook veel vezels welke zich bij de laterale pyramidebaan voegen.

Pyramidevezels eindigen in alle segmenten van het ruggemerg, maar de meeste toch wel in de beide intumescenties. Gelijktijdig ontstaan er afdalende spinale vezels welke zich bij de pyramidebaan voegen, maar hun aantal is niet voldoende om de geëindigde pyramidevezels te vervangen. Deze spinale vezels maken de degeneratie in de pyramidebaan sterker na een spinale dan na een corticale laesie. Bovendien bleek zeer duidelijk dat deze afdalende propriospinale vezels in de laterale pyramidebaan verder afdalen in het ruggemerg dan de pyramidevezels zelf. De veronderstelling is nu geopperd dat deze propriospinale vezels de pyramidale impulsen relayeren en op deze wijze een groter ruggemergsgebied beïnvloeden dan verwacht kan worden van de lengte der pyramidevezels. De corticospinale vezels dalen niet verder af dan het vijfde lumbale segment, terwijl de propriospinale vezels tot de meest caudale segmenten kunnen worden vervolgd.

De rubrospinale baan bleek te bestaan uit dikke vezels, welke verspreid lagen over een groot driehoekig gebied in de funiculus lateralis. Vele dunnere vezels dalen tezamen met hen af uit de hersenstam het ruggemerg in, maar deze hebben een andere oorsprong. De rubrospinale vezels vermengen zich spinaal op aanzienlijke wijze met de laterale pyramidale en met de ventrale spinocerebellaire vezels. De rubrospinale vezels kunnen worden gevolgd tot in de laagste sacrale segmenten.

Het bleek dat de fasciculus longitudinalis medialis een zeer complex vezelsysteem was, waarbij de vermenging van vezels van verschillende oorsprong de voornaamste eigenschap was. De fasciculus bestaat voornamelijk uit dikke vezels in de hersenstam, terwijl dunne vezels zich daar pas bij voegen in een laag medullair niveau. Deze dunne vezels zijn voornamelijk reticulospinale vezels. De meeste vezels van de fasciculus komen uit de vestibulaire kernen, en wel uit de nucleus medialis en descendens. Interstitiospinale vezels dalen in de fasciculus of tot het zevende cervicale segment, en tectospinale vezels tot het tweede thoracale segment. In het ruggemerg voegen zich dikke propriospinale vezels bij de fasciculus longitudinalis en laten deze er groter uitzien dan wanneer we alleen de supraspinale vezels beschouwen als samenstellers van de fasciculus. Deze supraspinale vezels

dalen het verst af in het ruggemerg, vergeleken met supraspinale vezels uit andere systemen.

De dikke vestibulospinale vezels liggen in een gebied van de funiculus anterior dat ook andere, dunnere vezels uit de medulla oblongata bevat. De meeste vestibulospinale vezels eindigen in de cervicale intumescentie, maar enkele kunnen worden vervolgd tot de lumbale intumescentie. Het is onmogelijk om in de thoracolumbale segmenten van een vestibulospinale baan te spreken, want deze vezels liggen ver uit elkaar langs de peripherie van de funiculus anterior en anterolateralis.

Het was onmogelijk scherp omschreven reticulospinale banen te localiseren. Reticulospinale vezels zijn overal aanwezig in de funiculi anterior en anterolateralis. De meeste reticulospinale vezels liggen in de gebieden van de afdalende banen, als de rubro- en vestibulospinale baan en speciaal de fasciculus longitudinalis medialis. Om de voorhoorn zijn verspreide reticulospinale vezels aanwezig, maar deze komen reeds niet meer voor beneden het tweede cervicale segment.

De fasciculus proprius bleek te bestaan uit dunne, korte, opstijgende en afdalende vezels in gelijke aantallen. Deze vezels zijn niet langer dan twee segmenten maximaal. Overigens zijn overal in alle systemen propriospinale vezels aanwezig, speciaal langere vezels liggen in de bekende banen. Zelfs in tot nu toe als homogeen beschouwde systemen, als de dorsale spinocerebellaire baan, blijken ze voor te komen.

Tenslotte kan worden opgemerkt dat in het ruggemerg *geen zuivere banen bestaan,* omdat naburige systemen hun vezels in aanzienlijke mate vermengen. Het verdient aanbeveling om de opvatting dat een baan zou bestaan uit een soort vezels van dezelfde aard te verlaten. Een betere definitie voor een baan zou zijn: *een gebied van witte stof met een specifiek vezelpatroon waarin vezels van een zeker karakter overwegen.* Echter is deze definitie in het geval van de fasciculus longitudinalis medialis niet helemaal juist. Vaak zal het beter zijn om van een vezelsysteem te spreken dan van een baan.

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